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Introduction

Introduction

1. Cadre conceptuel

Les grands herbivores, entre plantes et prédateurs (Olff et al., 1999), forment une partie importante des communautés de mammifères et ont donc une grande importance dans le fonctionnement des écosystèmes. En effet, les herbivores ont un impact direct sur la production primaire, par exemple en affectant la structure des communautés végétales et leur dynamique (Hester et al., 2006). Ils ont aussi une grande influence sur les cycles des nutriments parce qu'ils les redistribuent et agissent ainsi sur les propriétés du sol (Pastor et al., 2006). En outre, ils ont un impact sur les niveaux trophiques supérieurs qui se nourrissent d'eux (Andersen et al., 2006). Il est donc important d'étudier les populations de grands herbivores pour comprendre quelle influence ils peuvent avoir sur la structure et la dynamique des écosystèmes. Un point clé dans l'étude des grands herbivores est de comprendre quels facteurs font fluctuer leurs populations et pourquoi. Parmi les différentes disciplines de l'écologie, l'étude de la dynamique des populations peut fournir des informations sur les facteurs influençant les variations de l'abondance des populations et l'écologie comportementale peut être utilisée afin de déterminer comment les animaux s'adaptent à leur environnement.

Ces deux domaines de l'écologie ont longtemps été développés séparément, mais les écologistes tentent maintenant de relier le comportement des individus à la dynamique des population (Sutherland, 1996). En effet, la dynamique des populations est déconnectée des processus évolutifs, et n'a pas de théorie formelle qui peut permettre des prédictions sur la façon dont les écosystèmes vont évoluer. A l'inverse, les théories de l'écologie comportementale sont basées sur les processus de l'évolution par sélection naturelle : ces théories précisent qu'un comportement résulte d'une interaction complexe entre l'histoire évolutive des espèces, les événements qui ont eu lieu soit récemment dans les populations ou sont actuellement en cours, les caractéristiques des individus et les conditions dans lesquelles ils ont grandi (Danchin et al., 2008). Ceci permet d'extrapoler les effets que des conditions nouvelles peuvent avoir sur les populations, et pourrait être utilisé par exemple pour prédire comment les populations vont réagir à la perte d'habitat ou au changement climatique. La combinaison de la dynamique des populations et d'informations provenant de l'écologie comportementale nous permet ainsi de déterminer les paramètres démographiques importants des populations, mais aussi de mieux comprendre les processus derrière ces paramètres.

Deux approches différentes, qui ne sont pas exclusives, coexistent en dynamique des populations. La première est plus théorique et utilise la modélisation comme outil pour simuler des variations de taille de population et tester des théories sur les effets de différents paramètres démographiques sur ces variations. La seconde est basée sur l'analyse de données empiriques et a pour objectif d'expliquer les variations observées dans les effectifs de population, en identifiant les facteurs qui influent sur la dynamique des populations. Il est nécessaire d'utiliser à la fois ces concepts théoriques pour avoir des cadres de pensée dans lesquels émettre des théories générales sur comment différents processus peuvent agir sur les populations animales, mais aussi d'appliquer et tester ces concepts sur le terrain pour améliorer notre connaissance de l'écologie des espèces. En écologie comportementale, trois approches principales sont utilisées pour étudier les relations entre le comportement, l'écologie et l'évolution (Danchin et al., 2008). La première approche, qui a été - et est toujours - largement utilisée, est l'approche phénotypique. Cette approche ne teste pas directement des scénarios évolutifs, et suppose que l'étude du niveau phénotypique est suffisante pour déterminer les pressions de sélection sur les organismes. Elle est basée sur le concept d'optimisation : les organismes, à travers leur comportement, essayent de maximiser leur valeur sélective par rapport à d'autres organismes de la même population. Elle permet d'estimer les pressions de sélection qui agissent actuellement sur certains traits comportementaux. L'approche génotypique tente de mieux prendre en compte les mécanismes génétiques responsables des comportements, contrairement à l'approche phénotypique qui tend à considérer le déterminisme génétique des comportements comme une boîte noire (Grafen, 1984). Enfin, l'approche comparative est basée sur la comparaison des traits comportementaux entre espèces actuelles, afin de juger de l'adaptivité des ces traits ; cette approche peut permettre la reconstruction de scénarios évolutifs de différents traits. Ces trois approches sont, bien entendu, complémentaires, et leur utilisation dépend principalement des objectifs des études. En combinaison avec la dynamique des populations, l'approche phénotypique est d'un accès plus aisé et peut être utilisée pour déterminer quels processus agissent directement sur les individus et peuvent avoir un effet sur la dynamique des populations.

Comme mentionné précédemment, les études en dynamique de population chez les mammifères visent à expliquer comment et pourquoi l'abondance de ces animaux fluctue.

C’est un point clé dans l’identification des facteurs limitants et régulant ces populations. Comme ils consomment à la fois la production primaire et sont mangés par des prédateurs, la dynamique des populations de grands herbivores est à la fois sous l’effet « top-down » des prédateurs, mais aussi sous l’effet « bottom-up » de la production primaire. Pour les grands herbivores, les processus « bottom-up » représentent les effets des variations quantitatives et qualitatives de la production primaire sur la dynamique de leurs populations. Les processus « top-down » se référent à l’impact des prédateurs sur la démographie des grands herbivores. La régulation des populations de grands herbivores par les prédateurs ou les ressources a longtemps été débattue dans la littérature, et l’accent mis sur l’un ou l’autre est souvent une question de la perspective et du système d’étude préféré par les chercheurs (Hunter & Price, 1992). Aujourd’hui, il semble y avoir un consensus sur le fait qu’il n’y a pas de dichotomie entre ces deux effets, et que c’est l’interaction entre ceux-ci qui détermine les densités de population des herbivores. La question est maintenant plutôt devenue « Quels sont les facteurs modulant la limitation des ressources et la prédation dans le système étudié, pour déterminer quand et où les prédateurs ou les ressources vont dominer dans la régulation des populations ? » (Hunter & Price, 1992). Cependant, peu de choses sont encore connues sur la façon dont les prédateurs peuvent affecter la dynamique des populations de grands herbivores. En effet, les études les plus détaillées sur les grands herbivores sont situés dans l’hémisphère nord, souvent dans des endroits où ces herbivores n’ont pas de prédateurs. Ces écosystèmes anthropisés comptent peu de prédateurs et ont subi une grande influence de l’homme (Andersen et al.,2006). A l’inverse, les savanes africaines comportent encore une importante diversité de grands herbivores et de grands carnivores (Fritz & Loison, 2006). Des études récentes situées dans l’hémisphère sud ont en effet suggéré que les prédateurs peuvent avoir une influence importante sur la dynamique des grands herbivores (Sinclair et al., 2003 ; Grange et al., 2004). La taille de l’espèce proie semble être un facteur important dans la régulation par les prédateurs, Sinclair et al. (2003) et Fritz et al. (2011) ayant montré que la prédation avait des répercussions importantes sur les populations d’herbivore pesant moins de 150 kg. Pour les espèces de taille moyenne, les attentes sont moins claires, car elles se situent juste au-dessus du seuil à partir duquel Sinclair et al. (2003) prédisent pour les proies le passage entre une limitation par les prédateurs à une limitation par la nourriture. Bien que l’on sache que les prédateurs peuvent limiter les populations de proies, seulement quelques exemples de grands herbivores limités par leurs prédateurs sont donc bien documentés.

De plus, la prédation n'a pas qu'un effet numérique sur les proies. En effet, de plus en plus d'études montrent que les prédateurs peuvent affecter non seulement directement les proies en les tuant, mais peuvent aussi influencer leur comportement et induire des réponses physiologiques ou morphologiques (Lima & Dill, 1990 ; Creel & Christianson, 2008) ; les proies développent en effet des stratégies anti-prédatrices visant à réduire la prédation. Ces réponses, toutefois, sont coûteuses et peuvent donc, indirectement, affecter la démographie des proies ; ces coûts pouvant se manifester par une diminution de la survie, de la reproduction ou encore de la croissance des proies (Fig. 1). Un concept important pour mieux comprendre pourquoi développer des réponses anti-prédatrices peut être coûteux est le concept de compromis évolutif. Ce concept de compromis tient compte des besoins contradictoires auxquels l'animal doit faire face en situations naturelle, comme se nourrir mais également ne pas s'exposer aux prédateurs. Même si les deux comportements peuvent être exprimés simultanément, cela se traduit généralement par une efficacité diminuée par rapport à la situation où un seul comportement peut être exprimé (Futuyma & Moreno, 1988). Ainsi, par exemple, un animal investissant dans un comportement anti-prédateur ne peut pas investir autant dans la reproduction. Les effets qui n'agissent pas directement sur la dynamique des populations de proies ont été regroupés sous le terme effets indirects de la prédation.

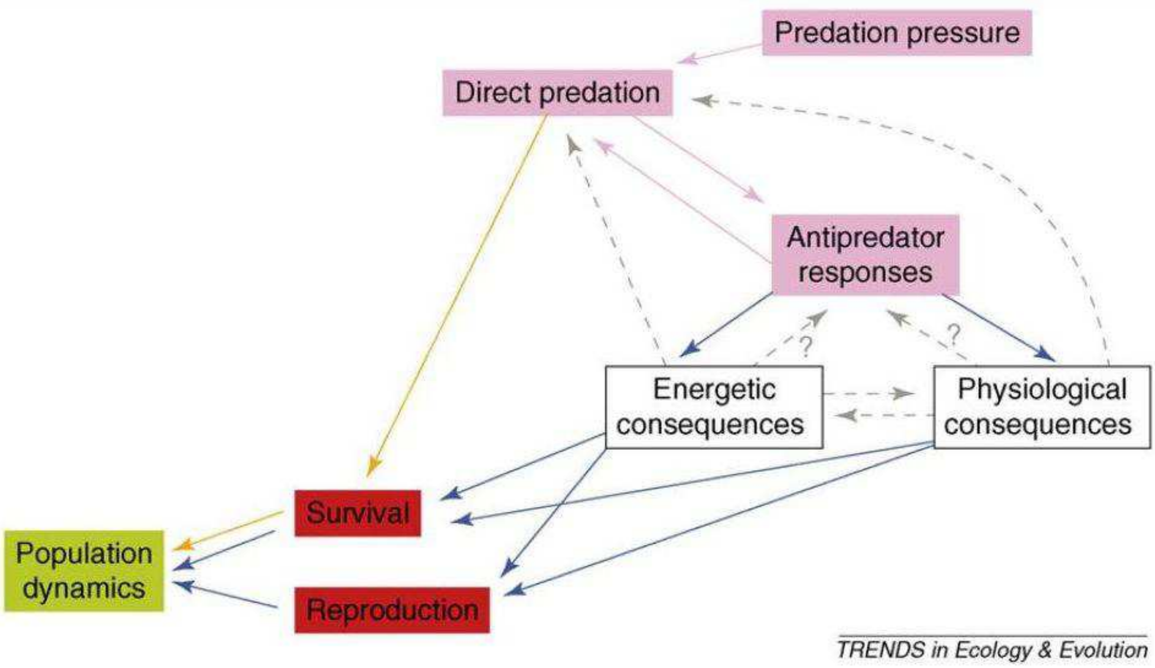

Figure 1. Voies par lesquelles la prédation peut affecter la dynamique des populations de proies. En orange, l'effet direct de la prédation sur la survie. En bleu, les effets indirects potentiels de la prédation. Tiré de Creel & Christianson (2008).

Il a été montré que ces effets indirects de la prédation ont parfois un effet important sur la dynamique des proies (Preisser et al., 2005). Nelson et ses collègues (2004) ont démontré en manipulant artificiellement la capacité de prédateurs à se nourrir de leur proie, que la mortalité des proies augmentait avec la seule présence des prédateurs : ils ont mis des pucerons en présence de punaises amputées de leurs pièces buccales. La simple présence des prédateurs a réduit de 30% la croissance de la population de pucerons par rapport à un témoin sans prédateurs. Le coût pour développer des stratégies anti-prédatrices n'est donc pas négligeable et doit être pris en compte dans l'étude des relations proies-prédateurs. En outre, de nombreux modèles de dynamique des populations ne tiennent pas compte de la variabilité entre individus. Cette variabilité peut avoir un rôle important dans la susceptibilité individuelle à la prédation (Pettorelli et al., 2011) : les proies individuelles ne sont pas égales dans leur susceptibilité à la prédation. Il a été démontré, par exemple, chez les wapitis *Cervus elaphus canadensis* que les individus les plus âgés souffrent d'un risque plus élevé de prédation que les adultes matures (Wright et al., 2006). Il a été également montré que mâles et femelles peuvent subir des taux de prédation différents (Fitzgibbon, 1990) ; plus généralement, les caractéristiques individuelles jouent un rôle important dans l'élaboration des réponses des individus. Mais pas seulement, car il existe aussi une variabilité individuelle, même entre individus qui partagent un grand nombre des mêmes caractéristiques. Le concept de personnalité décrit cette cohérence intra- et interindividuelle dans les comportements aussi bien temporelle qu'entre différents contextes (Sih et al., 2004 ; Bell, 2007). Cette plasticité limitée (Dingemanse et al., 2010) a été observée dans une grande variété de taxons (Bell et al., 2009). La personnalité peut influencer un large éventail de comportements, y compris des comportements anti-prédation (Quinn & Cresswell, 2005 ; pour une revue, voir Bell et al., 2009). Il est donc probable que la personnalité peut également avoir un effet sur la susceptibilité individuelle à la prédation. Les relations entre proies et prédateurs sont complexes, car elles combinent à la fois effets directs et indirects, mais dépendent également des différences individuelles, autant chez les proies que chez les prédateurs. Il est donc important d'essayer de comprendre les effets de la prédation au niveau de la population, mais aussi de prendre en compte les réponses individuelles au risque de prédation.

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2. Plan de la thèse

Dans cette thèse, j'ai exploré comment la prédation peut avoir un impact sur un grand herbivore en travaillant à deux échelles différentes : l'échelle de la population en utilisant des outils de dynamique des populations et l'échelle des individus, en me concentrant sur les changements de comportement dus à la prédation et à leurs coûts associés. Ce travail a été axé sur l'interaction entre une proie et un de ses prédateurs : le zèbre des plaines *(Equus quagga)* dans le parc national de Hwange au Zimbabwe et son interaction avec les lions.

Les deux premiers chapitres visent à mieux comprendre le fonctionnement de la dynamique de la population de zèbres dans notre zone d'étude. Jusqu'à présent, la plupart des études sur les taux de fécondité de grands herbivores ont été basées sur l'examen de l'appareil reproducteur d'animaux abattus. Dans le chapitre I, avec des collègues, nous montrons comment une méthode non-invasive (en utilisant des stéroïdes présents dans les fèces) peut être utilisée pour décrire la gestation chez les zèbres et permettre la détection des grossesses. Dans la deuxième partie de ce chapitre, je montre comment, en combinant ces données sur les hormones avec les données issues d'observations sur le terrain, l'intervalle entre deux naissances chez les zèbres femelles peut être mesuré, permettant ainsi d'en déduire un taux de fécondité de la population. Je discute également les facteurs qui pourraient influencer cette durée entre deux naissances consécutives. Dans le chapitre II, en combinant l'utilisation de méthodes de capture-marquage-recapture et de modèles de population matriciels, avec des collègues de l'équipe, nous analysons l'impact de la prédation par les lions sur les zèbres. Les méthodes de capture-marquage-recapture (CMR) sont de plus en plus utilisées, car elles sont le meilleur moyen pour obtenir des estimations précises des taux de survie (Lebreton et al., 1992). Il y a en effet un réel manque de données précises sur les taux vitaux chez le zèbre des plaines (Hack et al., 2002). Cette étude démographique basée sur des méthodes de CMR est la première sur le zèbre des plains en Afrique.

Dans les chapitres III à V, je me concentre sur les comportements anti-prédation des individus et sur leurs coûts pour les zèbres. Il a été démontré que le comportement de vigilance diffère entre les sexes dans certaines espèces, mais on en sait peu sur la façon dont ces différences peuvent entraîner des différences dans les coûts de la vigilance. Dans le chapitre III, j'analyse si la vigilance a un coût en termes d'alimentation et si ces coûts diffèrent entre mâles et femelles, en analysant le comportement de vigilance et le nombre de bouchées chez différents individus. Dans le chapitre IV, je teste expérimentalement l'impact d'un risque de prédation élevé sur la structure de la vigilance des zèbres, et je discute de l'influence des facteurs environnementaux et de la personnalité des zèbres sur la vigilance. Enfin, les effets du risque de prédation sur le régime alimentaire des grands herbivores ont été rarement étudiés. Dans le dernier chapitre, j'ai donc combiné des informations en temps réel sur la position des zèbres et des lions en utilisant la technologie GPS, avec des informations sur l'alimentation des zebra obtenues par échantillonnage de leur fèces, afin de discuter de l'impact possible de la présence de lions sur le qualité de l'alimentation des zèbres.

3. Modèle d'étude et site d'étude

3.1 Modèle d'étude

Présent dans la nature seulement en Afrique, le zèbre des plaines est le plus abondant des équidés sauvages et est également celui avec la distribution la plus large (Hack et al., 2002). Bien que son aire de répartition ait diminué au cours des 25 dernières années (Fig. 2), cette espèce n'est pas considérée comme en voie de disparition et est inscrite comme espèce à préoccupation mineure sur la liste rouge des espèces menacées de l'UICN (Hack & Lorenzen, 2008). Les zèbres des plaines se nourrissent principalement de graminées, et sont donc le plus souvent associés à des zones ouvertes comme les prairies et les savanes boisées. Les zèbres sont dépendants de l'accès à l'eau, car ils ont besoin de boire au moins une fois par jour ; ils sont donc généralement près de sources d'eau. Leur système de digestion par fermentation fait qu'ils utilisent une stratégie différente pour extraire l'énergie de leurs ressources alimentaires par rapport aux ruminants, ce qui peut leur permettre de subsister sur du fourrage de mauvaise qualité (Duncan, 1992) En outre, le zèbres des plaines est une espèce sociale : son système social est semblable à celui des autres équidés sauvages (Klingel, 1974; Rubenstein, 1986). Les zèbres vivent en harems, une structure sociale qui est susceptible d'influer sur leur démographie.

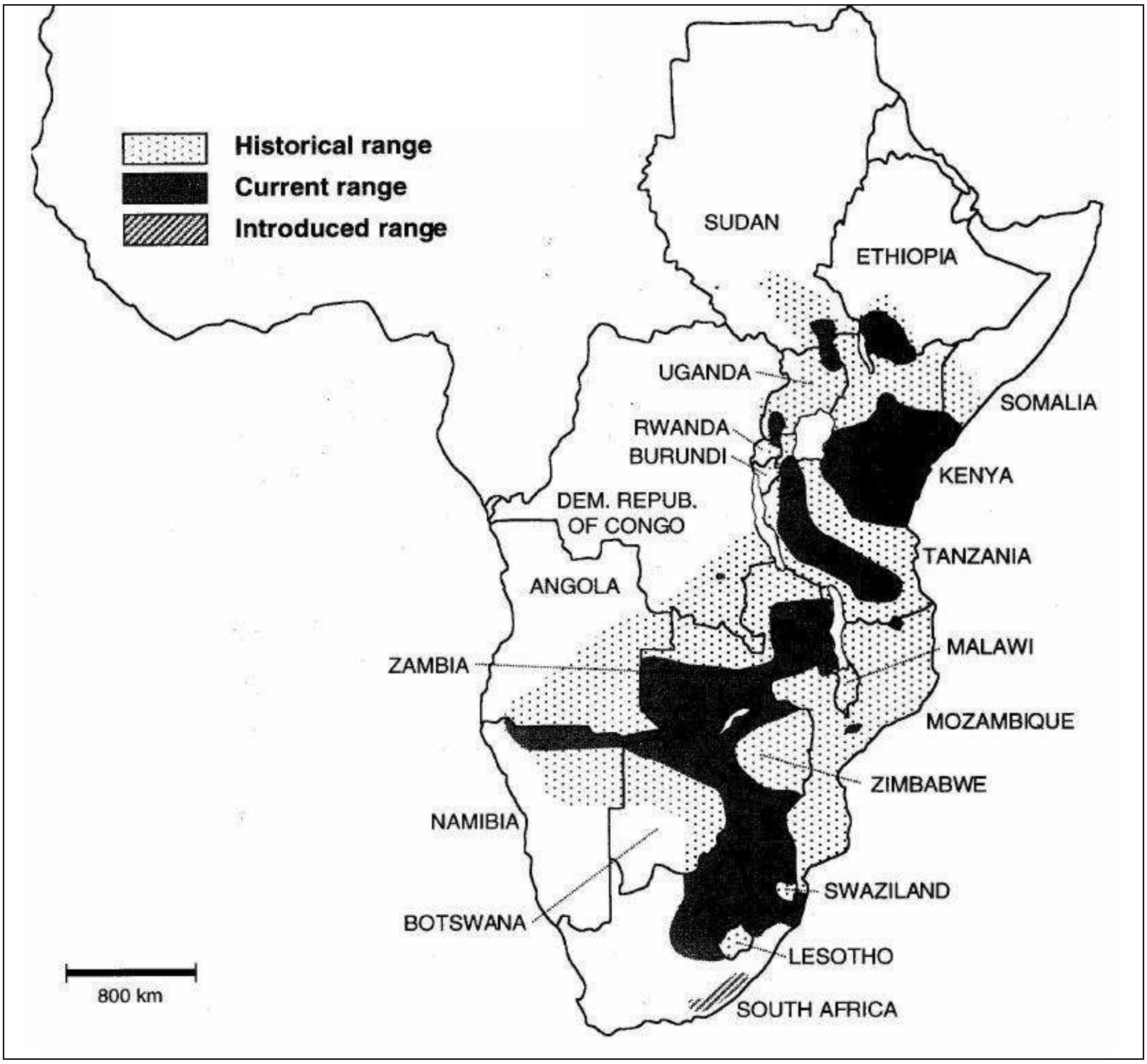

Figure 2. Carte historique et actuelle de répartition du zèbre des plaines. Tiré de Hack et al. (2002).

Les études sur le zèbre des plaines ont été principalement axées sur leur comportement social (Klingel, 1967; Klingel, 1969a) et leur reproduction (Klingel, 1969b ; Smuts, 1976a). La dynamique de populations des zèbres de plaines dans le Kruger a été étudiée en détail (Smuts, 1976b), mais il y a encore un réel manque de données précises sur les paramètres démographiques de cette espèce. Bien que le système social et les stratégies de reproduction des zèbres des plaines aient été largement étudiés, peu d'études ont documenté spécifiquement la dynamique de population de zèbres et peu de choses sont connues sur les facteurs régulant ou limitant qui agissent sur leurs populations (Hack et al., 2002). Parmi celles-ci, des études ont montré que certaines populations sont plus limitées par les ressources (Georgiadis et al., 2003) alors que d'autres ont montré l'influence importante possible de la prédation (Grange et al., 2004). À ce jour, il n’existe aucune étude avec des informations au niveau individuel sur les populations suivies.

3.2 Zone d’étude

Le parc national de Hwange est situé dans le nord-ouest du Zimbabwe et couvre une superficie d’environ 15000 km ^{2} (Fig. 3). Situé sur le bord du désert du Kalahari, ce parc est une savane semi-aride, où le sol est pauvre en éléments nutritifs. Le climat de Hwange est typique de ces savanes. L’année est divisée en trois saisons : une saison des pluies entre Octobre et Avril (98% des précipitations annuelles en moyenne), une saison sèche froide de Mai à Août, et une saison sèche chaude en Septembre, s’étalant jusqu’en Octobre en fonction de l’arrivée des pluies. La pluviométrie annuelle moyenne à long terme (de 1928 à 2005) est de 606 mm. En raison de la forte saisonnalité de l’environnement, la disponibilité en eau varie considérablement au cours de l’année. Pendant la saison des pluies, l’eau est disponible pratiquement partout dans le parc. Au cours de la saison sèche les points d’eau se tarissent et seuls certaines sources et certains lits de rivières retiennent de l’eau. Des pompes ont été installées à certains points d’eau, pour permettre le pompage des eaux souterraines et avoir de l’eau disponible tout au long de la saison sèche. Ces points d’eau pompés contribuent à maintenir une densité relativement élevée de grands herbivores au cours de cette saison. Ces trous d’eau artificiels sont principalement situés dans le nord et l’est du parc. Le parc est couvert principalement par des forêts (49,7%) et des arbustes (41,9%), avec des zones de prairies (8,4%) (Rogers, 1993). La végétation est typique de la savane dystrophique et est composée d’une mosaïque de différentes espèces ligneuses (les plus courantes étant *Acacia* spp., *Baikiaea plurijuga, Combretum* spp., *Terminalia cericea)* avec des prairies situés en bas des vleis et autour des points d’eau.

Figure 3. Emplacement du parc national de Hwange en Afrique Australe (en rouge).

Selon des recensements aériens, la population de zèbres du parc de Hwange a diminué de façon significative entre 1990 et 1999 de 4193 à 2155 (Grange, 2006), mais il n’existe pas de chiffres récents sur la taille de la population dans ce parc. Le parc contient une guilde complète de prédateurs, comprenant des lycaons, des hyènes, des léopards, des guépards et des lions. Toutes ces espèces peuvent potentiellement attaquer les zèbres. Les zèbres sont, cependant, l’une des proies de prédilection des lions, représentant 7,1% des proies tuées par ceux-ci (Periquet et al., 2012), et dont l’abondance par rapport à d’autres espèces de grands carnivores est élevée (en omettant les hyènes). Il est donc probable que la prédation par les lions sur les zèbres ait un impact plus fort que la prédation par d’autres espèces de carnivores. Depuis Juillet 2004, un suivi des individus d’une sous-population de zèbres est effectué tous les six mois dans la zone de Main Camp, dans partie nord-est du parc. Ce suivi est effectué pendant la saison des pluies (Janvier à Février / Mars) et pendant la saison sèche (Juillet à Août / Septembre) chaque année.

Section A

Dynamique de la population de zèbres des plaines dans la région de Hwange, Zimbabwe

Chapitre I

Taux de reproduction des zèbres dans le parc national de Hwange

Partie 1

Pattern of faecal 20-oxopregnane and oestrogen concentrations during pregnancy in wild plains zebra mares

Pattern of faecal 20-oxopregnane and oestrogen concentrations during pregnancy in wild plains zebra mares

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ABSTRACT

Regulative endocrine mechanisms influence the reproductive behaviour and success of mammals, but they have been studied predominantly in domestic and captive animals. The study aims at describing the pattern of faecal 20-oxopregnane and oestrogen concentrations during pregnancy in wild plains zebra *Equus quagga chapmani*. Data were collected during wet and dry seasons 2007-2009. Enzyme Immunoassays were used to determine 20-oxopregnane and oestrogen concentrations in faecal samples (n=74) collected from individual mares (n=32) whose dates of foaling were known through long-term monitoring. Hormonal profiles were described with a General Additive Model (GAM: Hormone ~ Days to Foaling). Faecal 20-oxopregnanes have a complex cycle during pregnancy (GAM, n=70, R^2=0.616, p<0.001). From -250 days to foaling, faecal 20-oxopregnane concentrations were above the baseline levels found in non-pregnant mares, peaking in the last 50 days. Faecal oestrogen levels showed a clear peak in mid-pregnancy (GAM, n= 62, R^2=0.539, p<0.001). The sex of the foetus and season had no detectable effect on hormone concentrations during pregnancy. High levels (>200ng/g DW) of faecal 20-oxopregnanes associated with high (>160ng/g DW) faecal oestrogen levels indicate mid-pregnancy in c. 90% of cases (16/17). High faecal 20-oxopregnanes (>200ng/g DW) and low faecal oestrogen levels (<160ng/g DW) indicate late pregnancy, again in c. 90% of cases. Two faecal samples would allow the stage of pregnancy to be determined with confidence.

Keywords: Oestrogen; 20-oxopregnane; reproduction; non-invasive method; pregnancy diagnosis; *Equus quagga*.

1 INTRODUCTION

Endocrine mechanisms regulate the reproductive physiology of mammals, which in combination with genetic, social and ecological factors influence individual fitness and reproductive behaviour. As a consequence, variation in reproduction can influence population survival such that an understanding of reproduction is essential for conserving species, populations and, indirectly, ecosystem functioning. Although reproductive physiology has been extensively studied in domestic and captive mammals [33], less is known about reproduction in wild populations, largely due to sampling difficulties. Non-invasive hormone monitoring methods using faecal samples have been used increasingly over the last 20-25 years both because of logistic feasibility and for welfare considerations since the welfare implications of collecting blood samples wild animals are increasingly recognized, e.g. [15,35]. Faecal sample analysis is now considered as a reliable method after being tested on several mammal species in captivity [4,7,14], and has been used for pregnancy diagnosis in the field [22].

Among non-human mammals, most work on the physiology of reproduction has been done on Ruminantia (including bovids) and Perissodactyla (including equids); two major groups of ungulates which have evolved in parallel [36]. The Perissodactyla, including seven extant species of equids, are much less studied than the Ruminantia, with hormonal cycles only described in detail for the horse [1]. Among wild species, the basic patterns are known in the endangered Grevy's zebra *Equus grevyi*, where oestrogen levels have been observed to be ten times higher in pregnant mares than in non-pregnant females and in male conspecifics, similar to the horse [3,31]. These patterns in faecal oestrogens are similar to plasma measurements, with a marked increase in levels of oestrogen after the first trimester [24]. Consequently, a study of four captive plains zebra mares showed that total unconjugated oestrogen concentrations measured by RIA could be used to diagnose pregnancy during the second and third trimester [37]. Progesterone levels increase above baseline levels during mid-pregnancy [16,26], but can show a biphasic pattern with an initial rise followed by a gradual decline, with a later second peak in both horses and zebras, e.g. [16,17]. Such a pattern may be associated with the formation of a secondary corpora lutea [17].

The plains zebra is an important component of large herbivore savannah communities, and is widely distributed throughout East and Southern Africa [11]. However, during the last decades, plains zebra populations have been extirpated from several parts of their range [12].

So far, studies on plains zebra have focused on social behaviour and reproduction [19,20,21,40], and little is known of their population dynamics [10,23], and, in particular, survival and reproductive rates [12]. Moreover, the patterns of reproductive hormone concentrations have not been described in wild plains zebra. Shot specimens have been used in some studies to determine the reproductive status of animals and to estimate fecundity rates [10,40], but non-invasive methods are clearly preferable. Enzyme Immunoassays (EIAs) for progesterone and oestrogens have been shown to be a reliable method to determine the reproductive status of other equids, including Grevy's zebra [3,6], wild and feral horses [4,22], and domestic horses [14,32], producing patterns that mirror plasma measurements, e.g. [16,24]. The overall aim of the present study was to examine the endocrine function of wild plains zebra mares, by describing the patterns of 20-oxopregnane and oestrogen concentration during pregnancy. Using measurements of faecal oestrogens and 5ß-pregnane-3α-ol-20-one concentrations, the study further aims to determine whether these techniques can be used to diagnose pregnancy in wild plains zebra, information essential to determine reproductive rates in wild populations.

2 MATERIALS AND METHODS

2.1 Study area

The study was conducted in the Hwange National Park (14,651 km^2), centred at 18°45'S and 26°45'E in south-western Zimbabwe. The plains zebra population investigated ranged within 40 km of Main Camp, about a fifth of the reserve. Altitude ranges from 900m to 1100m. Rainfall averages 640mm annually and is distributed within a wet summer season from November to April, with a precipitation peak reached in February, and a dry winter season [5]. The study area is generally flat and characterised by Kalahari sands, with occasional sand dune relicts, and includes vleis and patches of open grasslands. The vegetation consists mainly of woodlands and bush-lands dominated by *Baikiaea plurijuga*, *Combretum* spp., *Acacia* spp., and *Colophospermum mopane* [41].

2.2 Field observations and sample collection

The study employed an individual-based technique to investigate the endocrine status of mares (n=32) from a sample population (N=208) of free ranging plains zebra with known life histories. The individuals were identified by their unique stripe patterns that serve as a reliable key [28]. The field study began in 2004 and spans both wet and dry seasons. Faecal samples for endocrine analysis were collected from January 2007 till February 2009. The study animals were habituated to the presence of vehicles, facilitating behavioural observations and sample collection. As re-sightings of individuals were opportunistic, the foaling date was taken as the mid-point between the earliest and latest possible dates of birth estimated from the size of the foal when it was first seen, using the criteria of Smuts [39] and Penzhorn [27]. The precision was less than ± 30 days for almost all samples except two.

In heavily pregnant mares, the swelling of udders was used as an indication of closeness to foaling and thereafter re-sighting efforts were increased to try and estimate the date of foaling accurately. Suckling and maternal behaviour were used to determine maternity [18]. Since conception dates were not known, the number of days to foaling was estimated by backdating by the mean gestation period of the plains zebra (375 days [21]) from the estimated date of foaling.

In total, 74 samples were collected between 2007 and 2009 from 32 mares (mean ±SE = 2.31 ± 1.26 samples per mare; range = 1 to 6 samples per mare). In each case, mares were observed defecating, and no stallion had urinated on their faeces. A representative sub-sample of the faecal bolus were collected in the field, amounting to 100g each and dried within 48 hours, either by air or in a low heat (40^0C) field oven. The samples were packed in plastic bags and stored dry at room temperature until assayed (as in [14]).

2.3 Faecal extraction and hormone assays

Dried faecal samples were pulverized and sifted using a nylon mesh strainer to remove fibrous material as described by Fieß et al. [9]. Approximately 0.1 g of the faecal powder was extracted by vortexing for 15 minutes with 80% ethanol in water (3 ml). Following centrifugation for 10 minutes at 1500g, supernatants were transferred to glass tubes, ready for hormone analysis. The resulting extracts were measured for unconjugated oestrogens and 20-oxopregnanes using enzyme immunoassays for oestrogens (E_t, [25]) and 5ß-pregnane-3α-ol-20-one (5ß-20-one, [34]), which have been previously used to reliably diagnose pregnancy in mares of domestic equids [26]. Assay procedures followed standard protocols (e.g. described by Schwarzenberger [34]). Sensitivities (90% binding) of the assays were 1.0 pg/well for E_t and 0.3 pg/well for 5ß-20-one, respectively. Intra- and interassay coefficients of variation ranged between 6.4% and 9.3% for E_t, and 6.4% and 16.7% for the 5ß-20-one measurements.

2.4 Statistical Analysis

A Generalised Additive Model (GAM) [Hormone (Y) ~ Days to Foaling (X)] was used to describe the profiles of 20-oxopregnane and oestrogen concentrations during gestation. The GAM is described as $E(Y) = s_0 + s_i(X_i) + \ldots + s_j(X_j)$, where $s_i(X)$, $i = 1, \ldots, j$ are smooth functions [13]. The model computes a general non-parametric function that relates the predicted Y values to the predictor values [38]. The GAM was necessary in order to deal with pseudoreplication and to separate any effects on hormone levels of the various independent variables.

The day of foaling was designated Day 0. Samples were described with reference to the day of foaling. Four data points with abnormally low 20-oxopregnane values in late pregnancy were excluded as repeat samples of the same animals showed high levels, with three of the repeats within 2 weeks in the same pregnancy.

Since the hormonal data were not normally distributed, they were log transformed by $Y' = Log_{10}(Y)$. As a result of the complex nature of the 20-oxopregnanes distribution curve, a local General Linear Mixed-effect model (GLMM) was used to test the effects of fixed factors on levels of 20-oxopregnanes, and take into account the variability caused by repeated measures on individual mares. The pregnancy period was analysed in two phases, during early to mid-pregnancy (-375 to -100 days to foaling) and late pregnancy (-100 to 0 days to foaling). A GLMM was first used to test the effect of season and sex of the foetus as fixed factors and mare identity as a random variable on concentrations of 20-oxopregnanes. In addition, another GLMM with a 2nd order term was used to test for the fixed effects of sex of the foetus and season on oestrogen during pregnancy; and mare identity was included as a random effect. Statistical significance of all tests was set at $\alpha = 0.05$ and computed using R-version 2.9.0 software [30].

3 RESULTS

3.1 20-oxopregnane pattern for pregnant and non-pregnant mares

The relationship between the stage of pregnancy and concentration of faecal 20-oxopregnanes was non-linear (estimated degrees of freedom, >1.0). The GAM showed a significant effect of days to foaling (DTF) ($p<0.001$) and explained 65.9% of the deviance (Table 1). It allowed us to describe a complicated polynomial relationship between faecal 20-oxopregnane concentration and DTF, throughout the pregnancy and post-partum (Figure 1). The levels of faecal 20-oxopregnanes increased from -250 days to foaling, with a peak in the last 50 days. Immediately after foaling, levels of faecal 20-oxopregnanes declined sharply, with levels reaching baseline values almost immediately.

Formula	**20-Oxopregnanes ~ s(Days to foaling)**			
Parametric coefficients:	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	2.41655	0.04899	49.32	<2e-16 ***
Significance of smooth terms- s(Days to foaling)	Edf		F	p-value
	7.738		13.24	3.11e-11 ***
	R-sq.(adj.)	Deviance explained	Generalised cross validation score	N
Model	0.616	65.9%	0.19199	70

Table 1: Summary table for the Generalised Additive Model of the faecal 20-oxopregnane levels in plains zebra mares.

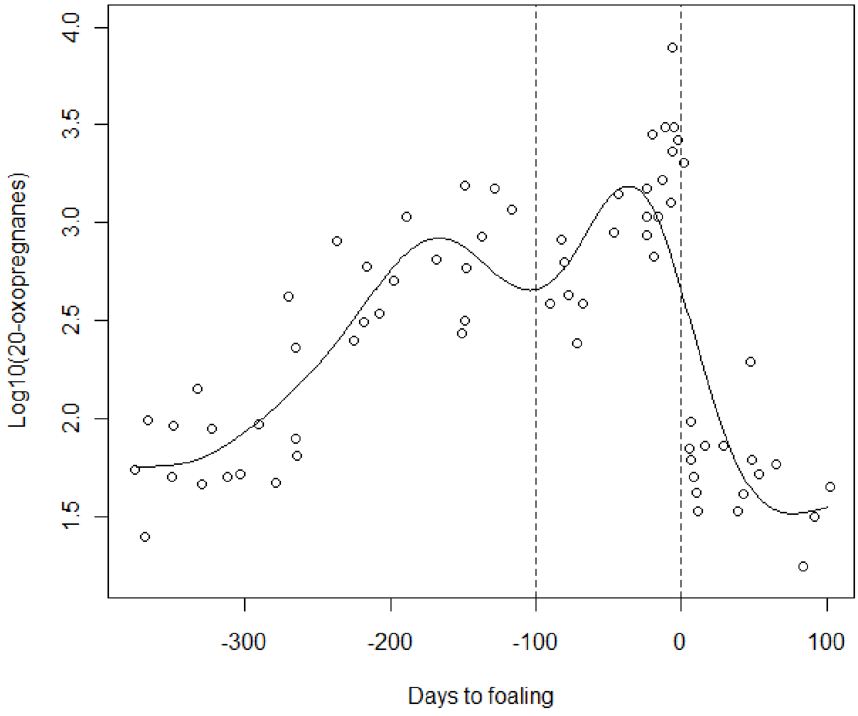

Figure 1: Log transformed concentrations of faecal 20-oxopregnanes (ng/g DW) in plains zebra mares before and after foaling.

3.2 Effects of season and sex of foetus on levels of 20-oxopregnanes

According to the pattern of faecal 20-oxopregnane levels described in the previous analysis, the effects of season and sex of the foetus were tested on the two main stages of pregnancy (early-mid and late) with contrasting patterns of this hormone, using Generalised Linear Mixed Models (GLMM) to take into account individual variability. In these GLMM, the effects of DTF, sex of the foetus and season (dry/wet) were tested. There was a significant effect of DTF in early-mid (p=0.001) and late (p=0.030) pregnancy stages. Sex of the foetus (p=0.654) and season (p=0.151) had no significant effect on the levels of faecal 20-oxopregnanes in early-mid pregnancy or in late pregnancy (sex (p=0.382) and season (p=0.470)).

3.3 Oestrogen pattern for pregnant and non-pregnant mares

The GAM for oestrogen also showed a significant effect of DTF (p<0.001), and was efficient in describing the levels of faecal oestrogen in mares, explaining 56.8% of the deviance (Table 2). The relationship was polynomial (order 2), with a clear peak in faecal oestrogen levels in mid-pregnancy (Figure 2).

Formula	**Oestrogen ~ s(Days to foaling)**			
Parametric coefficients:	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.9766	0.0444	44.52	*<2e-16* ***
Significance of smooth terms: s(Days to foaling)	Edf 4.830		F 14.55	p-value *4.89e-09****
	R^2-(adj.)	Deviance explained	Generalised Cross Validation score	N
Model	0.539	56.8%;	0.12221	62

Table 2: Summary table for the Generalised Additive Model of faecal oestrogen levels in plains zebra mares.

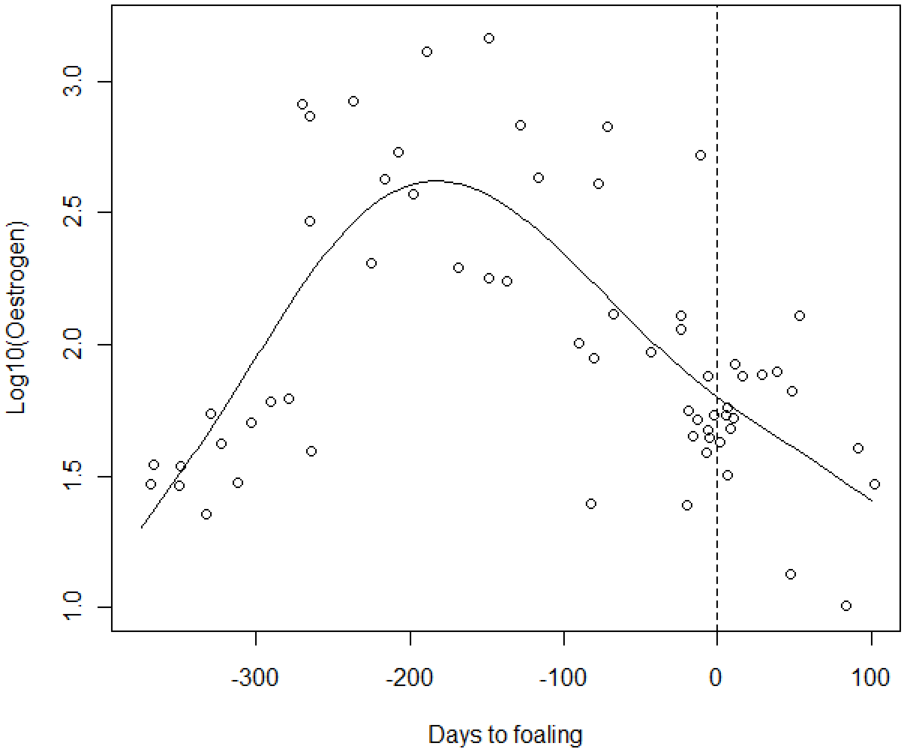

Figure 2: Log transformed concentrations of faecal oestrogens (ng/g DW) in plains zebra mares before and after foaling.

3.4 Effects of season and sex of the foetus on oestrogen levels

According to the pattern of faecal oestrogen concentrations described in the previous analysis, the next analysis was done during pregnancy only (n=45) using GLMM with a 2nd order term, in order to take into account individual variability. We tested for the effects of the sex of the foetus and season. The GLMM indicated a significant effect of DTF (p=0.001) and squared DTF (p<0.001). The sex of the foetus (p=0.671) and season (p=0.170) had no significant effect.

4 DISCUSSION

We describe for the first time the patterns of faecal 20-oxopregnanes and oestrogen concentrations throughout pregnancy in wild plains zebra. The gradual increase of faecal 20-oxopregnane concentrations to levels above baseline values (<200ng/g DW for non-pregnant mares) during mid-pregnancy (-250 to -100 days to foaling), resembles the pattern of progesterone levels observed in domestic horses [26,32]. In addition, the high 20-oxopregnane (>200ng/g DW) levels were maintained throughout mid-pregnancy, reaching a peak in late pregnancy (-100 to 0 days to foaling), as observed in horses [32], where they maintain pregnancy, suppressing foetal tissue rejection. The fall in the level of faecal 20-oxopregnanes immediately after foaling can be attributed to the loss of the foetal-maternal interface [1,8], since a greater proportion of progesterone during gestation is released by the allantochorion lining the myometrium [43]. Furthermore, the biphasic faecal progestagen pattern we recorded has previously been reported in zebras [17] and may be associated with the formation of a secondary corpora lutea.

In contrast to 20-oxopregnane, faecal oestrogen levels during pregnancy rise above baseline levels of non-pregnant mares (<160ng/g DW) after about 250 DTF, reaching a peak in mid-gestation, followed by a gradual decline until parturition; a trend consistent with the pattern observed in horses [4,32]. The rise and fall of faecal oestrogen levels in mid-pregnancy (Figure 2) coincides with the enlargement and subsequent regression of foetal gonads in equids [26]. A similar pattern in oestrogen concentrations during pregnancy has been observed in Grevy’s zebra [3,6,31], where foetal gonads synthesize large amounts of dehydroepiandrosterone, which initiates the production of oestrogen by the placenta [32]. The pattern of faecal oestrogen levels found in these wild zebras is similar to that described for the captive ones [37], although we found a gradual decline in levels from mid-pregnancy to foaling. Faecal extracts therefore appear to be an adequate source of steroid hormones for describing the gestational patterns of 20-oxopregnanes and oestrogen in zebras, as in other mammals.

Few studies have investigated the effects of seasonality on steroid hormone concentrations. In this study of wild zebras, in spite of the strongly seasonal environment, no seasonal effects were found in faecal 20-oxopregnane or oestrogen levels. Contrasting results have been found in other large herbivores: in the savannah elephant *Loxodonta africana*, faecal 5α-pregnane-3-ol-20-one levels increase in the wet season coinciding with an increase in food availability [42]. In Holstein–Friesian cows in Europe, different amounts of grass intake did not influence faecal progesterone metabolite concentrations significantly [29]. Another study showed that rats on a high plane of feeding had excreted more oestrogen in the faeces [2], and Schwarzenberger [32] postulates that factors such as compartmentalization, turnover rates, permeability and nutritional stress influence levels of faecal steroid metabolites in horses. Therefore, the potential seasonal effect of faecal progestagen and oestrogen metabolite excretion in wild zebra needs more attention, because out of the 52 samples from pregnant females, only 16 were from the dry season.

The GAM described the pattern of each hormone well, accounting for over 60% of the variance in the data. The models describing patterns of both hormones enable the detection of the reproductive status of plains zebra mares. High levels of 20-oxopregnanes (>200ng/g DW) associated with high oestrogen levels (>160 ng/g DW) indicated mid-pregnancy in 90% of cases (16/17, from data in from Fig. 1 and 2) and high 20-oxopregnane and low oestrogen levels (<160 ng/g DW) indicate late pregnancy, again in 90% of cases. Two faecal samples collected three months apart should therefore allow the pregnancy status of mares to be ascertained with confidence.

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Partie 2

Inter-birth interval in zebras is longer following the birth of male foals than after female foals

Inter-birth interval in zebras is longer following the birth of male foals than after female foals

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ABSTRACT

Mammalian reproductive rates vary among individuals for physiological and environmental reasons. This study aims to determine reproductive rates from an individually monitored population of wild Plains zebras *Equus quagga*, and to assess the sources of variability in inter-birth intervals. The animals were monitored, where possible, every six months from 2004 to 2011. Thirty nine intervals corresponding to 65 births in 26 mares were identified, using direct observations and faecal steroid monitoring. Mean foaling rate of the population is 0.74 foal/year, and comparable with the literature. There was no significant effect of mother's age, nor of the season of previous birth on the length of inter-birth intervals. Inter-birth interval was significantly longer when the first foal was a male. This finding indicates that additional costs of having a son may delay future reproduction and thus reduce the total number of offspring a mare can have during her lifetime. Individually-based data provide critical information on the determinants of reproductive rates, and are therefore a key to understanding the causes of variations in life-history traits.

Keywords: *Equus quagga*, Reproduction, Inter-birth interval, Foaling rate, Non-invasive hormone monitoring, Sex

1. INTRODUCTION

The dynamics of animal populations are affected by variations in rates of survival, reproduction and dispersion (Caughley, 1977). Processes acting on these rates operate at the individual level: understanding how these processes affect the life histories of individuals is therefore essential in order to understand the dynamics at the population level.

Reproduction is a process requiring large amounts of resources: since their availability varies in time and space, animals are generally limited by the amounts they can allocate to any one process. When investing in offspring, females make a trade-off between the growth of the offspring and their own growth and/or body reserves, and thus their chances of survival and of reproducing successfully in the future (Stearns, 1992). For example, in ungulates, the increased foraging demands caused by the high energy costs of lactation can jeopardize the females' own survival (White and Berger, 2001). Spreading reproductive events over longer time intervals can provide a period of recovery after reproduction during which females can finish their growth and/or accumulate body reserves and thus invest in their survival and prepare future reproductive output (Proaktor et al., 2008). Variations in the length of the interval between consecutive births can therefore provide valuable information about the costs of reproduction, and about the determinants of the levels of reproductive investment made by individual females.

Few studies have looked at the interacting factors influencing the interval between birth and conception of individual animals in the wild, essentially because of the lack of continuous observation of known individuals (but see Bercovitch and Berry, 2010). This study is part of a long term programme aimed at understanding the dynamics of the savannah ecosystem in the Hwange region of Zimbabwe, and the processes limiting a populations of herbivores are central in the programme, We have measured reproduction and survival in Plains zebras (*Equus quagga*) using a long-term, individually-based approach.

Reproductive rates in Plains zebra populations have been determined in only two previous studies, and in both cases by examining shot animals: in the Kruger National Park the pregnancy rate was 79% (Smuts, 1976) and in the Serengeti 88% (Grange et al., 2004). In this paper we describe a non-invasive approach for measuring reproductive rates in a population of wild Plains zebras, by calculating the mean foaling rate of the population, and subsequently testing for sources of variation in the inter-birth intervals of individually observed females. Previous studies on free-ranging horses and captive plains zebras showed that reproduction in mares, including birth sex-ratios, can be affected by factors such as maternal age, which can have a powerful influence on investment in reproduction by mares (Pluhacek et al., 2006).

Plains zebra are common herbivores of African savannahs, distributed from East to Southern Africa (Moehlman, 2002). They foal throughout the year and their gestation length is just over a year (with a mean gestation length of 371.2 days, Wackernagel, 1965). The minimum interval between foaling and conception is 8 - 10 days (King, 1965) and the shortest intervals between consecutive births so far observed were 378 and 385 days (Klingel, 1969); Wackernagel (1965) estimated the mean interval to be 13.9 months (417 days). Variability in the inter-foal interval therefore exists, but there is no information on the determinants of this variability in wild Plains zebras.

Zebra females can foal at three years of age, but they may grow until six years of age (Smuts, 1975), so we hypothesise that the trade-off between growth and reproduction would lead to longer inter-foal intervals in young females. Further, older females can be expected to have different intervals compared to prime-aged animals: the intervals could be lengthened through the process of senescence. This was true in the Serengeti, as senescent females had lower reproductive rates than prime age females (Grange et al., 2004).

The environment of Hwange is highly seasonal, with average annual rainfall of 606mm, of which only 10mm fall during an average dry season which lasts 6 months (May-October, Valeix et al., 2007). Dry season births are likely to be more costly due to the poor availability of adequate resources, thus females giving birth during this season may need more time before conceiving again. In the Kruger National Park, which has a similar environment to that of Hwange, Plains zebras have a clear birth peak in the wet season (Smuts, 1976): a longer inter-foal interval after a dry season birth could be a mechanism leading to more frequent foaling in the wet season, we therefore expected to find longer intervals after foals born in the dry season in our population. Finally, intervals should be longer after giving birth to a male foal, as males are generally more costly to raise in mammals (Bercovitch et al., 2000; Fernàndez-Llario et al., 1999; Rutkowska et al., 2011) including horses (Duncan et al., 1984; Cameron and Linklater, 2000).

In this paper, we report the duration of intervals between births in a population of Plains zebra, calculate the foaling rate, and attempt to disentangle the factors determining the length of the inter-foal intervals. We hypothesize that:

(1) The age of a female should influence the inter-foal interval, with younger and senescent females having longer intervals between successive births

(2) Females giving birth during the dry season should have a longer interval to the next birth

(3) The interval to the next birth should be longer after giving birth to a male foal

2. MATERIALS AND METHODS

2.1 Study area

The study was based in Hwange National Park, which covers approximately 15,000 km² of semi-arid savannah in western Zimbabwe (19°00'S, 26°30'E). Long-term (1928-2005) mean annual rainfall is 606 mm (Valeix et al., 2007) with a dry (May-October) and a wet (November-April) season. The vegetation is dominated by deciduous woodlands and shrublands, with patches of grasslands (Rogers, 1993). The presence of 30 artificial waterholes in the northern part of the Park in most years maintains drinking water, and a relatively high density of large mammals, particularly during the dry season. The study population of Plains zebra moved freely since there are no fences, within the Main Camp area (approximately 1,000 km²) in the northern part of the Park.

2.2 Field observations

Observations started in July 2004 and fieldwork sessions were conducted twice a year (around July-August during the dry season and around January-February during the wet season) up to March 2011. Zebras were identified individually from their unique stripe patterns. Re-sighting of animals was opportunistic, with a focus on waterholes and a plain where zebras often concentrate during the wet season. A database was built up which includes individual photos (both sides of each zebra) for recognition and the sightings of every animal.

Ninety females were identified and monitored to determine their pregnancy status using steroid concentrations in the faeces where possible (Ncube et al., 2011) and to have accurate estimates of their foaling dates. As re-sightings of individuals were opportunistic, not all foals were sighted immediately after birth: we estimated the age of the foal when first sighted using the criteria of Smuts (1974) and Penzhorn (1982). The foaling date was taken as the mid-point between the earliest and latest possible dates of birth with regard to these criteria. Neonatal mortality could be determined, but only for females which were followed closely: heavily pregnant females close to foaling have swollen udders, and if a foal is lost the udder involutes within about 5 days (Smuts, 1976). One pregnant female whose abdominal profile was no longer large and whose udders had been swollen and then returned to normal 5 days after, was noted as having foaled and lost her foal, as none was observed with her. Foaling date was taken as the mid-point between last sighting with swollen udders and the next sighting. Suckling and maternal behaviour were used to determine maternity, and the sex of the foal was determined as soon as possible after the first sighting. Mares of known age were classified into three age classes (Young 3-5, Prime: 6+ years) and a few obviously old females were classified as Senescent: old horses, like other large mammals show a number of characteristic features[1]. With personal experience of horses, one of us (P. Duncan) classed as Senescent animals which had “Sagging topline resulting in a 'sway' or dipped back with prominent withers”.

2.3 Faecal sample collection, extraction and hormone assays

In order to determine the pregnancy status between two observed births we collected dung samples from individuals (Ncube et al., 2011): 149 samples from 52 mares were collected from mares which were observed defecating, between January 2007 and March 2009 and analysed for 20-oxopregnane and oestrogen concentrations. We collected a sub-sample representative of the dung pile, and dried it within 48 hours, either air-drying or in a low heat (40^0C) field oven. The samples were packed in plastic bags and stored dry at room temperature until assayed.

Dried faecal matter was pulverized and sifted using a mesh strainer to remove fibrous material (Fieß et al., 1999). Approximately 0.1 g of each powdered faecal sample was extracted by vortexing for 15 minutes with 80% ethanol in water (3 ml) according to the procedure described by Ncube et al. (2011). The resulting extracts were measured for unconjugated oestrogens and 20-oxopregnanes using enzyme immunoassays for oestrogens (E_t; Palme and Möstl, 1994) and 5ß-pregnane-3α-ol-20-one (5ß-20-one; Schwarzenberger et al., 1996), which have been previously used to reliably diagnose pregnancy in Plains Zebra (Ncube et al., 2011). Assay procedures followed standard protocols (e.g. described by Ganswindt et al., 2002). Sensitivities (90% binding) of the assays were 1.0 pg/well for E_t and 0.3 pg/well for 5ß-20-one, respectively. Intra- and interassay coefficients of variation ranged between 3.1% and 9.3% for E_t, and 6.4% and 16.7% for the 5ß-20-one measurements.

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[1] For a summary of these features, see :
http://www.vetstream.com/dalehead/html/pdf/Factsheets/Horse/24_269864.pdf

2.4 Pregnancy determination

For females of unknown pregnancy status between two consecutive births, faecal steroid hormone concentrations were used to determine the possibility of a pregnancy. The criteria from Ncube et al. (2011) were used to ascertain the pregnancy status of the mare in between the two births: high levels (> 200 ng/g DW) of faecal 20-oxopregnanes associated with high (> 160 ng/g DW) faecal oestrogen levels indicate mid-pregnancy; high faecal 20-oxopregnanes and low (< 160 ng/g DW) faecal oestrogen levels indicate late pregnancy. At least two samples were used to ascertain the pregnancy status. Females which were determined to have had another pregnancy in the interval between the two observed births were removed from the dataset. Intervals between observed births which were longer than two mean gestation periods (740 days), and for which we did not have information on the pregnancy status of the mare were also excluded from the dataset. In total 65 births and 39 foaling intervals in 26 mares could be identified.

2.5 Statistical analyses

The intervals were not normally distributed (Shapiro-Wilk's test, $p < 0.01$), and were close to a Gamma distribution. We used a Generalized Linear Mixed Model (GLMM) using function glmmPQL of package MASS in R-software version 2.12.2 (R Development Core Team, 2011) specifying that the response variable follows a Gamma distribution. We treated age of the female (Young, Prime or Senescent), season of initial foaling (Dry or Wet), and sex of the initial foal (Male or Female) as fixed factors. The identity of the female was treated as a random factor. Effects were considered significant when $p < 0.05$. Only 38 intervals were used in the analysis, as the sex of one foal was unknown.

3. RESULTS

Births occurred in both wet and dry seasons. The mean interval between two births was 480 days (SE = +/- 116 days, range = 375-821 days). The average foaling rate of the population was therefore 0.74 foal/year (the foaling rate was calculated as 365/mean foaling interval). The sex-ratio at birth (21 males, 35 females) was not significantly biased ($\chi^2 = 3.5$, df = 1, $p = 0.06$), but mares tended to produce more females than males during our study period.

Interval lengths from young mares were not longer than intervals from prime age mares (Table 1, $p = 0.77$). There was no significant difference in the length of the intervals between senescent and prime mares (Table 1, $p = 0.11$).

The effect of season on interval length (p = 0.47) was not statistically significant, but intervals tended to be longer when the initial birth occurred during the dry season (Table 1). There was an effect of the sex of the foal (p = 0.04) on the length of the interval: intervals were longer when the initial foal was a male (Table 1, Fig. 1).

Model	N	Factors	P-value	Coefficient +/- SE
Effect of age, season and foal sex	38	Age		
		Young	0.770	-15.19 +/- 51.36
		Senescent	0.111	-69.33 +/- 41.78
		Season		
		Wet	0.470	-31.19 +/- 41.51
		Foal sex		
		Male	0.040	88.10 +/- 37.49

Table 1: Factors influencing the length of the interval between two consecutive births in female Plains zebras. Individual identity was included as a random factor. Age (Youn*g*, *Prime*, Senescent), Season of birth (*Dry*, Wet) and Foal sex (Male, *Female*) were considered as categorical (classes used as references are italicised).

4. DISCUSSION

The mean foaling rate of the Hwange zebras was 0.74 foals/year (95% c.l. calculated by bootstrap, n = 1000 repetitions, are 0.68 – 0.79). This reproductive rate is close to the best data in the literature, on the Kruger population (0.79, Smuts 1976). The Serengeti population may have a higher foaling rate (0.88, Grange et al., 2004), but this may be due to a biased sample, since unlike in the Kruger study there was no specific procedure to ensure that animals were chosen at random (see Grange et al., 2004). The use of individually based data therefore produces results which are consistent with previous studies; it can however be noted that due to the method used, some very long inter-birth intervals can be missed and lead to an over-estimation of the foaling rate.

We present here for the first time data on the patterns of variability in the interval between consecutive births in a wild population of Plains zebra, and one of the first in a wild ungulate (see Bercovitch and Berry, 2010). Inter-birth intervals depend mainly on the delay between foaling and subsequent conception, since gestation length varies only within narrow limits (Clements et al., 2011). Variation in the length of the inter-birth intervals was high (CV = 23%), and few females had the capacity to sustain successive pregnancies without a break (median interval length = 462 days). This is surprising as female horses in good condition commonly become pregnant in the post-partum oestrus, and so have an inter-foal interval of about 340 days (see Duncan, 1992), and the studied zebra mares were almost all in good or very good condition (scores 7-8 out of 9 on the scale of Henneke et al.,1983).

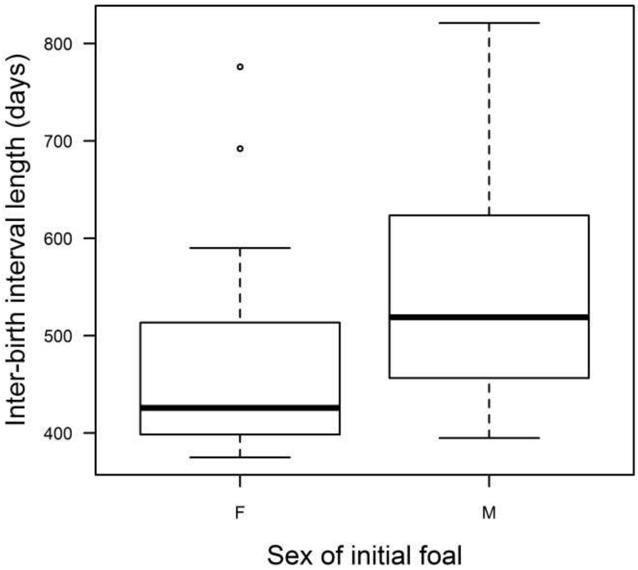

Figure 1. Length (in days) of the inter-birth interval as a function of the sex of the initial foal in the monitored Plains zebra population of Hwange National Park, Zimbabwe, between 2004 and 2011. F: Female, M: Male.

There was no significant difference between intervals beginning in the dry season with those beginning in the wet season. This may be due to the small number of births during the dry season (only 17 out of 65). However, only few females supported the cost of foaling during the dry season twice in a row (four females showed dry-dry series, out of twelve dry season births, i.e. 33%), so females may postpone reproduction to give birth to their next foal during the wet season. Some studies on horses have shown that resource limitation reduced the foaling rate in horses, though only in young ones (Duncan, 1992), however more data are needed to demonstrate a seasonal effect in zebras.

Contrary to our predictions, there was no difference in the average intervals of younger and senescent females compared to prime mares. This may be due to the small numbers of young (5) and senescent (5) individuals. In captive Plains zebras, age (and/or dominance) leads to shorter intervals (Pluhacek et al., 2006). If this result is general, then there was no trade-off between growth or body condition and reproduction, so even young and senescent females had abundant resources in these zebras in Hwange and in the captive population.

When females had male foals, the time between foaling and conception was lengthened on average by 88 days (Table 1, Fig. 1). The mares took time to recover after having a male foal, implying that males are more costly to produce. There were no differences in survival of male and female foals (Sophie Grange, unpublished results), so this can not explain the longer time needed by mares to conceive after giving birth to a male. It has been shown in another monomorphic Perissodactyl, the Black Rhino (*Diceros bicornis*), that the proportion of male calves surviving to their first sighting was positively associated with rainfall prior to and during the time of conception, so to food abundance and, presumably, the body condition of the mothers (Hrabar and du Toit, 2005). Male Black rhinos may therefore be more costly to produce than female, though this result could also be explained by lower intra-uterine and neonatal survival in male calves (see also Monard et al., 1997). As there is no sexual size dimorphism in Plains zebras at birth (Smuts, 1975), this greater energy demand by males cannot be explained by higher requirements of male foetuses during the gestation period, and the extra cost of male foals in zebras can come only after birth.

It has been shown in horses (Duncan et al., 1984), that male foals spend 40% more time suckling than females during the first eight weeks of their lives and, if males do obtain more milk, then they are more costly to produce; it has also been demonstrated that mares in good condition in two horse populations, raised more males (Cameron et al., 1999; Cameron and Linklater, 2000, 2007; Monard et al., 1997). Zebras live in harems, and adult males are subjected to intense competition for females, probably leading to a greater variance in reproductive success for males than for females. Investing more in males in early stages of development, at a cost, could result in better quality of the offspring which could persist into adulthood. Those males could thus be advantaged and have greater reproductive success than their competitors. This would corroborate the hypothesis of Trivers and Willard (1973), that females should bias investment towards the sex that can return greater fitness from additional investment.

There was no significant bias in the sex-ratio of the foals in this study, but a tendency for mares to produce more females. The same tendency was found in the whole monitored population, but still non-significant (58 females, 44 males in identified foals during 7 years of monitoring, $\chi^2 = 1.9$, df = 1, p = 0.17). The cost of having a male may therefore bias the sex-ratio at birth, and if females can control the sex of their offspring (see Clutton-Brock and Iason, 1986), mares would be producing more of the less costly females.

In conclusion, large differences exist in inter-birth intervals of zebra mares in the Hwange system, with some females conceiving immediately after giving birth and others waiting over a year before conceiving. This is comparable to findings of Klingel (1969), who observed 120 mares during three years and found that 15% of the females had three foals, 33% had two, and 42% had just one offspring. The cost of producing a son delayed future reproduction, which would reduce the total number of offspring a mare can have during its lifetime. This result supports the conclusion of Cameron and Linklater (2000) that male foals are more costly than females to equid mothers. However, the mechanism is not yet known, and may involve the provision of more milk, or behavioural costs (e.g. more vigilance after producing a male foal). More work is needed to disentangle the other factors determining inter-individual differences in zebra reproductive rates. In this regard, long-term individually-based data can provide the fine-grained data needed to deepen our understanding of how these factors interact to determine foaling rates.

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Chapitre II

Demography of plains zebras (*Equus quagga*) under heavy predation

Demography of plains zebras (*Equus quagga*) under heavy predation

Submitted to Ecology

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ABSTRACT

In natural ecosystems, densities of ungulate populations show strong temporal variations. The ecological processes driving these fluctuations are complex: food limitation and predation are both important, and they can interact. Survival rates are central to this debate, but data are sparse for tropical ecosystems. Here, we provide age- and sex-specific survival of plains zebra in the Main Camp area of Hwange National Park, a near-natural, nutrient-poor savanna in Zimbabwe with a complete community of predators and high predator-prey ratio. We estimated survival from a detailed Capture-Mark-Recapture (CMR) monitoring of 184 known individuals. We controlled for variations in detection probabilities among adult females, which resulted from their social structure. As expected, survival was low during the first year (0.370); increased in yearlings (0.624) and peaked at 0.795 and 0.847 in adult males and females respectively. Survival at all ages was low compared to ungulates without predators. The survival of adult females was lower during the dry season, which probably resulted from higher predation due to predictable movements of the zebras to waterholes. We then identified the demographic mechanisms driving this population. The demographic model we performed led to a declining population (λ=0.93), which was consistent with trends from road counts (λ=0.91). A LTRE analysis using the Serengeti population as a reference showed that the main cause of decline in the zebra of Hwange was low survival in yearling females; low foal and adult survival also contributed. In this ecosystem with a complete guild of large predators at high densities relative to prey, predation is likely to be the main ecological process causing low survival, and therefore the decline in the zebra population.

Keywords: CMR, equids, population limitation, predation, tropical ecosystems

Introduction

Ungulates are a central component of natural ecosystems, between plants and predators (Danell *et al*. 2006), so a good knowledge of their ecology is essential to understand the structure and functioning of ecosystems, and also for their conservation and management (Williams *et al.* 2002). Long-term studies on African ungulates show that their populations often experience strong variations (Sinclair and Arcese 1995, Du Toit *et al*. 2003). Dry season food resources influence juvenile mortality, and consequently population size, in several ungulates (Mduma *et al*. 1999, Owen-Smith *et al*. 2005). Likewise, predation plays an important role in the decline of some prey populations (Harrington *et al*. 1999, Power 2002, Tambling and Du Toit 2005). The ecological processes driving fluctuations of abundance in African ungulate populations are complex and not fully understood, and demographic parameters, especially survival, are of course central to this debate.

Most studies of survival in Northern hemisphere ungulates (Loison *et al*. 1999 on roe deer *Capreolus capreolus*, bighorn sheep *Ovis canadensis* and Pyrenean chamois *Rupicapra pyrenaica*, Coulson *et al*. 2001 on Soay sheep *Ovis aries,* Festa-Bianchet *et al*. 2003 on Mountain goat *Oreamnos americanus*, Catchpole *et al*. 2004 on red deer *Cervus elaphus*, Toïgo *et al*. 2007 on ibex *Capra ibex*) have used Capture-Mark-Recapture (CMR) analyses to account for imperfect detection, which is necessary to obtain unbiased estimates of survival (Nichols 1992, Lebreton *et al*. 1992, Gimenez *et al*. 2008). These studies have improved our understanding of population dynamics of several species, and have allowed the ecological and environmental factors that shape variation in survival to be identified. Longitudinal studies based on individuals have also been used to estimate survival patterns in African ungulates, such as kudu *Tragelaphus strepsiceros* (Owen-Smith 1990) and elephant *Loxodonta africana* (Moss 2001), but only two studies, on impala *Aepyceros melampus* (Gaidet and Gaillard 2008) and giraffe *Giraffa camelopardalis* (Suraud *et al*., In Press) accounted for imperfect detection by using a CMR method.

Amongst African ungulates, the plains zebra (*Equus quagga*) is a common species, widely distributed across East and Southern Africa. During the last decades plains zebras have been extirpated from parts of their range, and many populations have declined (Moehlman 2002). However, our understanding of their population dynamics is still rather limited (Hack *et al*. 2002). Their populations can be limited by top-down or bottom up processes, since resources limit plains zebra in Laikipia, where predator densities are low (Georgiadis *et al*. 2003), but in the Serengeti the zebra population is limited by low foal survival, apparently due to predation (Grange *et al*. 2004). In general, within African ungulate communities, zebras tend to be more sensitive to top-down processes than grazing bovids (Grange and Duncan 2006). In previous studies, survival patterns of plains zebra populations were assessed using life tables and age ratios (Spinage 1972, Georgiadis *et al*. 2003, Grange *et al*. 2004), so they are likely to be biased because of the strong assumptions inherent to the methods (see *e.g.*, Caughley 1977). As carcasses of juveniles disappear faster than adults, the young age classes are under-represented in the dead sample. There is therefore a need for accurate information on age- and sex-specific survival patterns to understand the population dynamics of plains zebra.

Here, we report the results of the first demographic analysis based on a CMR study on an African grazer, using the monitoring of individually known zebras between 2004 and 2011 in Hwange National Park, Zimbabwe. The main objective was to test the hypothesis that zebra survival in this near-natural ecosystem, including a complete guild of large herbivores and their predators, would be lower than in populations without predators. The population declined after 2005 (Figure 1), and we expected that it would be limited by low survival since the predation pressure on zebras is higher in Hwange compared to other African ecosystems (Table 1). Moreover, the study area in the northern part of Hwange shelters the highest densities of lions and hyenas in the Park (Loveridge *et al*. 2007a, Drouet-Hoguet 2007). Zebra survival was estimated for adult males, adult females, foals and yearlings: we expected low survival during the first year of life (as in the Serengeti, Grange *et al*. 2004), and lower survival in yearlings and adults than in predator-free populations. Like wild horses, zebra stallions compete for mates and protect their harems from predators (Klingel 1975) and in many equids, secondary sex ratios favor adult females (Berger 1983). We therefore expected a lower survival in adult males compared to females. Temporal effects (time, year and season) were tested on survival and detection probabilities: since there is practically no rain in the long dry season (6 months), we expected lower survival in the dry season, at least in yearlings, the age-class most sensitive to food shortages (as in the Serengeti zebras, Grange *et al*. 2004). Finally, we investigated which demographic parameters were the most influential in driving the observed demographic pattern. We first built a demographic model (matrix model, Caswell 2001) using age-specific survival obtained in that study and information on age-specific reproduction (Barnier *et al*., In Press). We then compared the population growth rate obtained from this demographic model with observed trends in the population during the study period. Lastly, we performed a Life Table Response Experiment (LTRE) analysis to measure the relative contribution of demographic parameters to the observed variation in the population growth rate (λ) between this zebra population (declining) and the Serengeti one (stable).

Study area	Ratio "predator/zebra"
Hwange	0.10
Kruger	0.08
Ngorongoro	0.03
Serengeti (migratory)	0.01

Table 1. "Predator/zebra" ratios in four African Parks. The ratios are based on the biomasses (kg/m^2) of zebras and five carnivore species present in these Parks (lion, spotted hyena, cheetah, African wild dog and leopard; see Fritz *et al*. 2011).

Material and Methods

Study area

Hwange National Park covers 14 651 km² in western Zimbabwe. This system is near natural as there is very little hunting in the Park by people, and commercial hunting of lions outside the Park was stopped between 2005-10 (Loveridge *et al*. 2010). This study was conducted in the Main Camp area (*ca*. 1500 km²) in the North western part of the Park and the adjacent Forestry area. The zebra density has been measured since 1999. The vegetation is typical of southern African dystrophic wooded savannas with patches of grasslands, and plant communities are dominated by *Colophospermum mopane*, *Combretum spp*., *Acacia spp*., *Baikiaea plurijuga* and *Terminalia sericea* (Rogers 1993). The long-term average annual rainfall at Main Camp is 606 mm, almost all falling from October to April (Chamaillé-Jammes *et al*. 2006). About 30 artificial waterholes have been dug in the northern and eastern parts of the Park, and these allow water-dependent large mammals to use the area year-round. Observations started in July 2004, and fieldwork sessions were conducted every six months (in July-August during the dry season and in January-February during the wet season) until February 2011. We identified and monitored zebras in the Main Camp area, where waterholes and an abandoned airstrip attract many grazers and provide a good visibility for field observations.

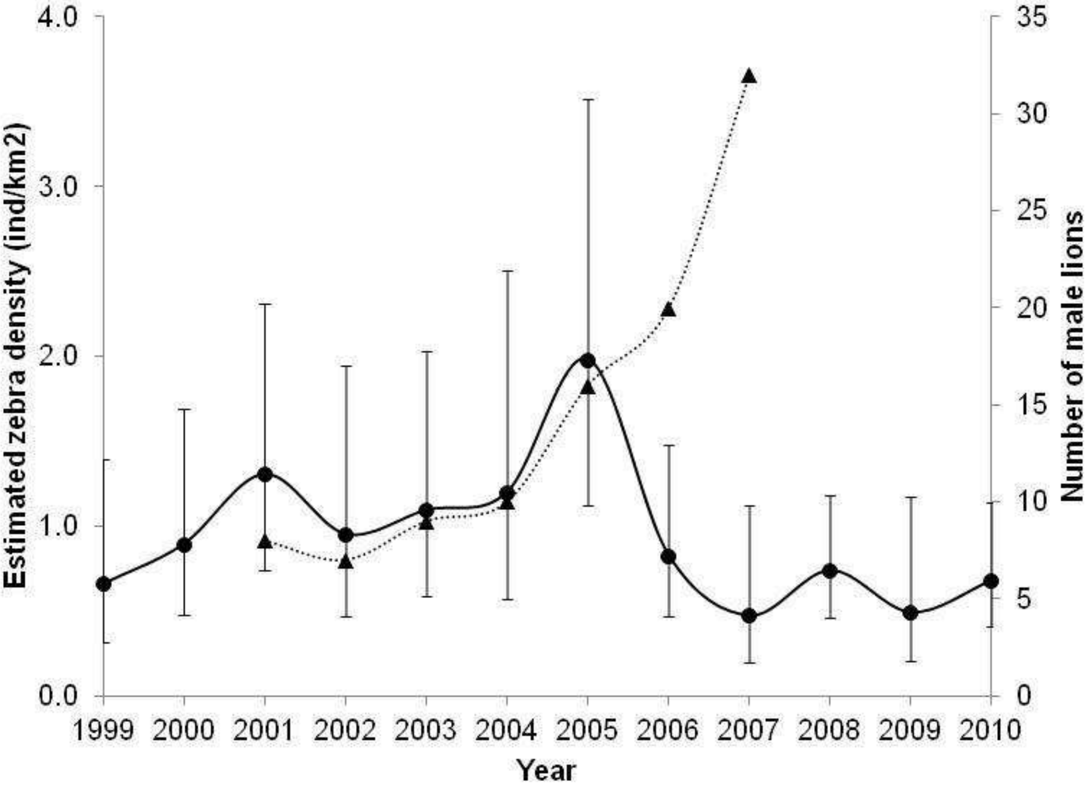

Figure 1. Zebra densities during the dry season (black circles; solid line) and number of adult male lions in the Main Camp area (black triangles; dotted line; data from Loveridge *et al*. 2010). Error bars represent 95% confidence intervals.

Identification and monitoring

Zebras were identified individually from variations in their stripe pattern (spots, irregular forks, especially the shoulder pattern; Klingel 1967). We estimated the age of the foals when first sighted using the criteria of Smuts (1975) and Penzhorn (1984), completed with photographs of foals of known age in this population. Foals (0-12 months), yearlings (12-24 months), and individuals over 2 years-old (adults) were separated for this analysis. A database was built and included over 11000 sightings, with photos of both sides of each individual, biological characteristics (age, body condition, predation marks, and reproductive status), and group composition. Fifty individuals (in 9 family groups) were first identified in July 2004. This database was updated continuously since then. CMR models were based on

184 individuals: 116 adults (36 males and 80 females of unknown age) and 68 individuals first identified as foals.

CMR modeling

The program U-CARE was first used to perform goodness-of-fit tests to detect problems in the data structure (Choquet *et al.* 2009a). The Cormack-Jolly-Seber (CJS) model was fitted on individuals first identified as adult males, adult females, and foals using E-SURGE (Choquet *et al.* 2009b). We incorporated additive and interactive combinations of temporal (time, year and season) and individual (spatial groups for mares, sex and age-class for young zebras) effects on both survival and detection probabilities (notations used in Lebreton *et al*. 1992).

Ungulates generally show a survival pattern with a marked age-structure, survival being low over the first year, increasing in yearlings, reaching a maximum during the prime-age stage, and declining at old ages (Gaillard *et al*. 2000). CMR models were therefore run either on individuals first identified as less than 6 months-old (foal stage) or as adults (≥2 years-old). For adult females, U-CARE tests indicated a problem with the structure of the data (global test: χ^2=114.378, df=33, p<0.001), due mainly to trap-dependence (statistic =-6.566, p<0.001). Social bonds between zebra mares are likely to have caused this heterogeneity in detection. We therefore performed a cluster analysis with R software version 2.12.0 (R Development Core Team 2011) to classify the adult females into different spatial groups according to the geographical locations where they were observed. This analysis defined 4 groups that were closely associated and used different parts of the study area. After including spatial groups, U-CARE tests still detected some problems in data structure (global test: χ^2=51.314, df=32, p=0.017), due to some heterogeneity in detection probability (statistic=-2.188, p=0.029). To take into account the heterogeneity in detection of the adult females, we used multi-event models in which detection probability varied randomly across time. These models distinguished between two states among living individuals: those with high detection probability (H) and those with low detection probability (L). In the study population, young zebras dispersed from their families at about 2 years of age (24.6 months ±1.2 SE; n=32). Using individuals first identified as foals, we built an age-dependent model based on three age-classes (foal: 0-1 year-old; yearling: 1-2 years-old, and adults: ≥2 years-old), considering that survival in the two first age-classes was not greatly affected by dispersal. We did not look for actuarial senescence because the oldest zebras whose age was known accurately were only

5 years of age. We also tested for between-sex and between-cohort differences in survival and detection probabilities.

In each case, we selected the model with the lowest Akaike information criterion (AIC). For adult females, multi-event models were classified according to QAICc (QAIC is the criterion modified for over-dispersed data; and "c" indicates a weighted QAIC for small sample size). Model averaging was then used for comparisons between selected models (Burnham and Anderson 2002). Statistical tests were used to detect differences between the mean values of parameters (survival or detection probability) across seasons and sexes.

Survival of the young

Monitoring was done every six months and births occurred all through the year in this population. Some foals were monitored from birth +/- 2 days (17.3%; n = 75), but most entered the database within their first two months (81.3%; n = 75). The CMR modeling based on individuals first identified as foals gave a biased estimate of first year survival since it cannot include foals that were born, but not observed in the field. A study of reproduction in mares conducted between 2007 and 2009 using hormone assays in 152 fecal samples provided reliable criteria to detect pregnancy (Ncube *et al*., 2011). These data allowed us to estimate the number of missed foals in the field when mares were detected pregnant but the foal was not seen alive. Using field observations on foals and pregnancy data on reproductive mares, we built a predictive model to calculate the probability of first-year survival depending on the age at first sighting. This model involved a logistic regression with observation after the age of 12 months as a binary response variable and age at first sighting as a dependent variable. When a pregnancy was detected, we marked the foal as being identified at birth (*i.e.* assuming that fetal loss is negligible, as supported by available data (<10% loss) in horses; Chevalier-Clement 1989). The analyses were performed using data from all foals born between October 2003 and March 2010, and the GLM function of the R-software (version 2.12.0, R Development Core Team 2011).

Population trends

We modeled the dynamics of this zebra population with a pre-breeding census matrix model (Caswell 2001). We used an age-structured model with 4 classes (0-1 year-old, 1-2 years-old, 2-3 years-old and ≥3 years-old) to account for the age at first reproduction in adult females. The model was based on females, assuming that male numbers were not limiting female reproduction. Age at first foaling was set at 3 years (Smuts 1976) and the sex ratio at birth was taken as balanced. Age-specific survival was derived from the CMR modeling (this paper) and fecundity from long-term monitoring of reproduction was estimated at 0.74 (females ≥3 years-old, Barnier *et al.*, In Press). The demographic model was run using the ULM software (Legendre and Clobert 1995).

We then compared the population growth rate obtained from the demographic model with the estimate from observed trends of population size derived from road transects conducted in the Park between 1999 and 2010. We estimated zebra density during the dry season using Distance Sampling software (version 4.1; Thomas *et al*. 2003). Annual population growth rate in year *t* is estimated as $\lambda = \frac{N_{t+1}}{N_t}$; where N_t is the population size in year *t* and N_{t+1} the population size in year *t+1*. The population growth rate over a given study period was calculated as $\lambda = \left(\frac{N_t}{N_0}\right)^{\frac{1}{t}}$; where N_0 represents the initial population size, N_t the population size in year *t*, and *t* is the number of years (Caughley 1977). Lastly, we performed a LTRE analysis to identify the most influential parameters accounting for the declining trend recorded in the studied population. We used the Serengeti population (Grange *et al*. 2004), which shows stable population size (λ close to 1), as a reference. LTRE analysis is a retrospective analysis (*sensu* Caswell 2001) that allows partitioning the difference of growth rates between a treatment (here zebra in Hwange) and a control (here zebra in Serengeti).

Results

Adult males

The best model for adult male survival included a seasonal effect on the probability of detection (Table 2), with detection probabilities varying from 0.746 (±0.049 SE; 95% CI: 0.640-0.830) in the dry season to 0.923 (±0.030 SE; 95% CI: 0.840-0.965) in the wet season. The annual survival of adult males was constant and estimated at 0.795 (±0.052 SE; 95% CI: 0.689-0.901) in the selected model, which was much more likely than the subsequent model with a seasonal effect on both survival and detection probabilities (AIC weight of 63% *vs*. 29%, respectively). Adult male survival tended to be lower in the dry season (0.871 *vs*. 0.911 in the six months of the dry and wet seasons respectively; ε=0.762).

Model $^{(*)}$	**n**	**Deviance**	**AIC**	**ΔAIC**	**AICweight**
Φ(i)p(ss)	**3**	**264.606**	**270.606**	**0.000**	**0.632**
Φ(ss)p(ss)	4	264.169	272.169	1.563	0.289
Φ(ss)p(yr)	9	260.083	278.083	7.477	0.015
Φ(i)p(i)	2	274.481	278.481	7.875	0.012
Φ(i)p(yr)	8	262.527	278.527	7.921	0.012
Φ(ss)p(i)	3	272.576	278.576	7.970	0.012
Φ(i)p(t)	14	250.681	278.681	8.075	0.011
Φ(yr)p(ss)	9	261.260	279.260	8.654	0.008
Φ(ss)p(t)	15	249.884	279.884	9.278	0.006
Φ(t)p(ss)	15	253.282	283.282	12.676	0.001

Table 2. Number of parameters (n), deviance, Akaike Information Criterion (AIC) and AIC weights of the 10 best models fitted for adult males. Bold lettering indicates the selected model.
$^{(*)}$ *Model notations: survival (Φ), detection probability (p), constant (i), time (t), season (ss) and year (yr).*

Adult females

The best model for adult female survival included interactive effects of season and group on the probability of detection (Table 3). The lowest detection probability of 0.392 (±0.058 SE; 95% CI: 0.286-0.509) was observed for the group 4 (20 mares) in the dry season while the highest detection of 0.985 (±0.015 SE; 95% CI: 0.902-0.998) occurred for the group 2 (21 mares) in the wet season. From the selected model, the seasonal survival of adult females varied between seasons: 0.864 (±0.024 SE; 95% CI: 0.809-0.905) in the dry season *vs*. 0.981 (±0.018 SE; 95% CI: 0.885-0.997) in the wet season (ε=3.865). The annual survival of adult females was therefore 0.847 (±0.027 SE; 95% CI: 0.794-0.900). The selected model accounted for 65% of QAICc weight (*vs*. 20% for the subsequent one).

Yearlings

The best model for yearling survival included an effect of year on the probability of detection (Table 4); which varied between 0.491 (±0.178 SE; 95% CI: 0.192-0.796) in 2007 and 0.969 (±0.024 SE; 95% CI: 0.867-0.994) in 2010. Yearling survival was constant over time (0.624±0.035 SE; 95% CI: 0.553-0.694). As in adult males, yearling survival tended to be lower in the dry season (0.763 *vs*. 0.819 in the 6 months of the dry and wet seasons respectively; $\varepsilon=0.593$). The difference between the sexes was not significant (0.643 *vs*. 0.604 for male and female yearling survival respectively; $\varepsilon=0.748$).

Model ^(*)^	**n**	**Deviance**	**QAIC**	**QAICc**	**ΔQAICc**	**QAICcweight**
Φ(ss)p(g*ss)	**11**	**648.367**	**670.367**	**673.548**	**0.000**	**0.654**
Φ(g+ss)p(g*ss)	14	642.693	670.693	675.943	2.395	0.198
Φ(ss)p(g+ss)	8	660.097	676.097	677.771	4.223	0.079
Φ(ss)p(t+g)	19	633.038	671.038	681.171	7.623	0.014
Φ(g*ss)p(g*ss)	17	640.431	674.431	682.379	8.831	0.008
Φ(g+ss)p(g+ss)	12	654.755	678.755	682.560	9.012	0.007
Φ(g)p(g*ss)	13	652.606	678.606	683.100	9.552	0.006
Φ(yr)p(g*ss)	16	644.315	676.315	683.290	9.742	0.005
Φ(g*ss)p(g+ss)	14	650.068	678.068	683.318	9.770	0.005
Φ(i)p(t+g)	18	638.379	674.379	683.379	9.831	0.005

Table 3. Number of parameters (n), deviance, Akaike Information Criterion corrected for over-dispersion (QAIC) and small sample size (QAICc), and QAICc weights of the 10 best models fitted for adult females. Bold lettering indicates the selected model.
(*) *Model notations: survival (Φ), detection probability (p), constant (i), group (g), time (t), season (ss) and year (yr).*

Foals

The survival probability increased with age at first sighting (slope= 0.008 ±0.003 SE; p=0.007), so the risk of mortality was high during the first weeks of life and then decreased with age thereafter (Figure 2). The probability of survival from 0 to 12 months of age was 0.370 (±0.051 SE; 95% CI: 0.269-0.472).

Model [(*)]	**n**	**Deviance**	**AIC**	**ΔAIC**	**AICweight**
Φ(a)p(a+yr)	**12**	**322.162**	**346.162**	**0.000**	**0.293**
Φ(a+ss)p(a+yr)	13	321.505	347.505	1.342	0.150
Φ(a+s)p(a+yr)	13	321.960	347.960	1.798	0.119
Φ(a+c)p(a+yr)	23	302.908	348.908	2.745	0.074
Φ(a*s)p(a+yr)	15	319.742	349.742	3.580	0.049
Φ(a)p(a+t)	18	314.185	350.185	4.022	0.039
Φ(a*yr)p(a+ss)	22	306.527	350.527	4.365	0.033
Φ(a*yr)p(a*ss)	24	302.617	350.617	4.454	0.032
Φ(a*yr)p(a+yr)	26	299.082	351.082	4.920	0.025
Φ(a)p(a+ss)	7	337.111	351.111	4.949	0.025

Table 4. Number of parameters (n), deviance, Akaike Information Criterion (AIC) and AIC weights of the 10 best models fitted for yearlings. Models are based on 3 age-classes (0-1 year-old, 1-2 years-old and ≥2 years-old). Bold lettering indicates the selected model.

[(*)] *Model notations: survival (Φ), detection probability (p), age (a), sex (s), cohort (c), time (t), season (ss) and year (yr).*

Demographic analysis and population trends

The data from transect counts show that the population declined during the study (Figure 1, λ=0.91 between 2004 and 2010). The population growth rate obtained from the demographic model was similar (λ =0.93). The mean generation time ($\bar{T}$) was estimated at 13.14 years.

The LTRE analysis showed that yearling survival contributed the most to the decline of the population in Hwange in comparison with the stable population in Serengeti (Figure 3). The results indicate that survival contributed more than recruitment (77% *vs*. 23%), and survival of yearlings (40%) and subadults (2-3 years of age: 33%) contributed much more than adult survival (3.5%). Removing the confounding effect of senescence (because senescence occurred in Serengeti but could not be estimated in Hwange), did not change markedly the pattern with the highest contribution for yearlings (32%) and subadults (27%) than for adults (22%). The generation time of zebras was much longer in the Hwange population (13 years) than in the Serengeti population (8 years) because survival in the non-reproductive young age classes was so low in Hwange.

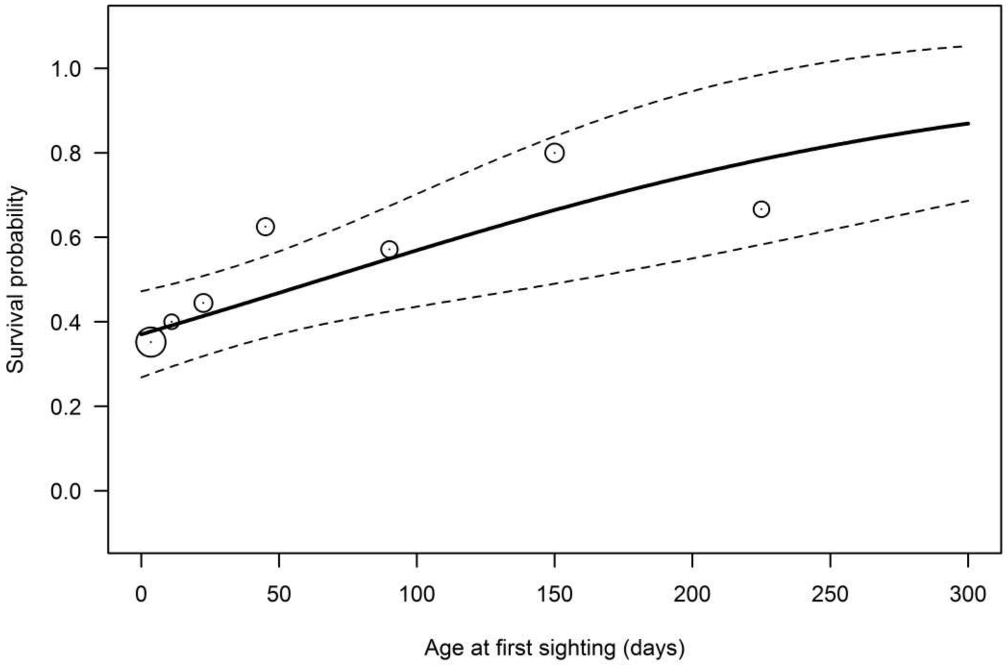

Figure 2. Logistic regression of the survival probability until one year of age in zebra foals, as a function of age at first sighting. Circles represent the proportion of surviving foals first seen at different ages (0-7 days, 1-2 weeks, 2 weeks-1 month, 1-2 months, 2-4 months, 4-6 months and 6 months to 1 year). The circle size is proportional to the sample size. The solid line represents the prediction of the model and the dotted lines the 95% confidence intervals.

Discussion

Detection probabilities

Detection probabilities were generally high, indicating that individual re-sightings were quite successful in the study area. These probabilities varied, since adult zebras were more easily detected during the wet season, when they concentrated on grasslands, than in the dry season when they were more dispersed. In young age classes (foals and yearlings), the probability of detection varied between years, with the lowest values in 2007 and the highest in 2010; probably due to variable conditions for observations. In adult females, detection probabilities were influenced by season and by the social structure: this analysis provides a first empirical demonstration of the necessity of accounting for the effects of social groups on detection probabilities to obtain unbiased survival rates.

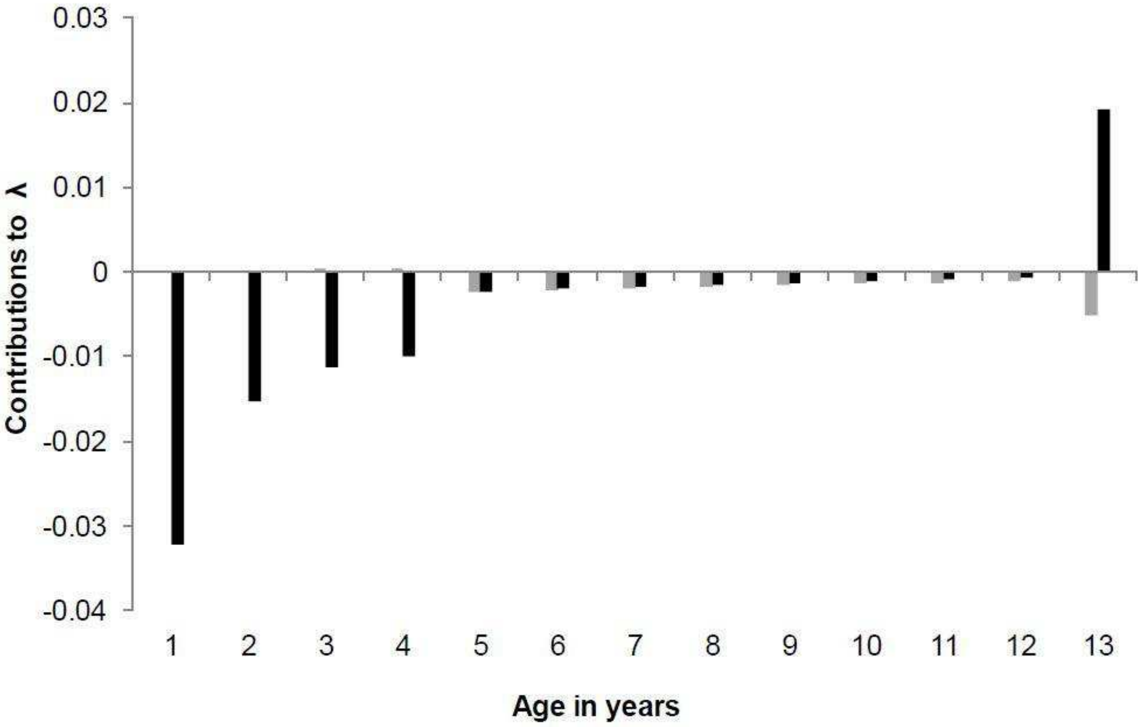

Figure 3. Contributions of age-specific recruitment (grey bars) and survival (black bars) rates to λ in female zebras in Hwange compared to the Serengeti.

Foal and yearling survival

Foal survival (0.37) was much lower than in wild and feral horse populations (0.83 in Kamainawa horses (Cameron *et al*. 2001), 0.81 in Przewalski horses (Tatin *et al*. 2009), and 0.62-0.95 in Camargue horses (Grange *et al*. 2009), but was quite similar to estimates of foal survival in zebras in Serengeti (0.389; Grange *et al*. 2004) and in Kruger (0.39-0.41; Mills and Shenk 1992), two African zebra populations coexisting with large predators. Foals in the Hwange population obtain milk from their mothers for 8-18 months (P. Duncan; pers. obs.), and should therefore not be strongly affected by seasonal variations in resource abundance, as occurs in other African ungulates, such as the white-eared kob, *Kobus leucotis* (Fryxell 1987).

Survival in yearlings was 0.624. The sex and the cohort of the animals had no effect, nor did season or year, in spite of the extreme seasonality, and the drought in 2005 (330.5 mm of rain in Main Camp, compared to the long-term annual average of 606 mm). Yearling survival (0.624) was much lower than in the Serengeti population (0.847; Grange *et al*. 2004; ε=6.312). The relative importance of mortality and dispersal is difficult to assess; during dispersal young zebras are likely to be more exposed to predation since they are not well integrated in a particular social group. An interaction between predation and dispersal could explain their low survival.

Adult survival

As in other equid populations (Berger 1983), the annual survival of adults was slightly lower in males than in females (0.795 *vs*. 0.847 respectively). Male competition was noticeable in this population, with at least two of the known males being injured severely when losing their harems (P. Duncan, pers. obs.). The survival of adult females was markedly lower during the dry season (0.864 *vs*. 0.981 in wet season). In this population, births occurred in both dry and wet seasons, inducing additional costs for reproductive mares during the dry season, a period when food and water were limited. Moreover, lactating mares need to drink more often than other zebras, spending more time at the waterholes where the risk of predation is high (Valeix *et al*. 2009b).

Our estimate of adult female survival (85%) is similar to the estimate for mature females in the Serengeti (0.875; Grange *et al*. 2004). The annual survival of 80 and 85% found in adult males and females at Hwange is low for a prime-age survival in an ungulate of this size: many studies on temperate ungulates indicated a prime-age survival over 90% (Gaillard *et al*. 1993, Loison *et al*. 1999, Coulson *et al*. 2001, Festa-Bianchet *et al*. 2003, Toïgo *et al*. 2007). However, none of these populations were affected by predation. In a CMR study on bighorn sheep populations experiencing declines due to predation, Festa-Bianchet *et al*. (2006) showed that prime-age survival varied from 0.720 to 0.914 in males and 0.792 to 0.899 in females. Consequently, the survival rates of adult zebras in Hwange are in the range expected for ungulate populations coexisting with large predators.

Ecological processes involved

In spite of the long dry season, zebras at Hwange are in good/excellent condition year-round (apart from wounded animals, they score 7-9 on the 9 point scale of Hennecke *et al*. (1983), so the availability of resources during the dry season did not seem to affect the body condition of the animals. The predation pressure on plains zebra is high in Hwange compared to other African savanna systems (Table 1). The zebra is also one of the top five prey species killed by lions in Hwange (Loveridge *et al*. 2007b). A recent study on lions in Hwange shows that the predation risk is particularly high in this study area, as the density of lions is high compared to the rest of the Park (Valeix *et al*. 2009a). A long-term study on spotted hyenas also showed that the Main Camp area has one of the highest densities of this large predator in Hwange (Drouet-Hoguet 2007). Consequently, predation risk on zebras is potentially even higher in the study area than elsewhere in the Park. Zebra densities declined during the study, settling at about 0.5/km², much lower than before 2005 (Figure 1). Trophy hunting was suspended in the hunting areas surrounding Hwange National Park in 2005-10, and the numbers of male lions in the study area increased after 2005 (Figure 1; Loveridge *et al*. 2010). Additionally, cub survival improved once trophy hunting was suspended, possibly due to the reduced turnover of territorial males (Loveridge *et al*. 2010). This suggests that an increase in the size of the lion population has occurred since 2005 in the study area, which was likely to increase mortality of prey species, such as zebras. Since, the lower survival of adult females observed during the dry season is unlikely to be caused by a decrease in body condition, the most probable cause is predation pressure around the few waterholes, where most lion kills are located (within 2 km, Valeix *et al*. 2009b). For water-dependent grazers, such as zebras, the need to regularly access the few active waterholes to drink during the dry season is likely to make them more vulnerable to predation by lions at this time of the year, since their movements are spatially predictable. Variability in the predator populations (temporal and/or spatial) could therefore explain why the Main Camp zebras were declining during the study period, but not before.

Demographic consequences of survival patterns

The demographic model predicted a decline in the study population (λ=0.93), which matched the decline observed in zebra densities in the Main Camp area between 2004 and 2010 (λ=0.91). Using a LTRE analysis, we found that survival had the highest contribution and was therefore the limiting factor, with yearling survival accounted for the largest decrease of growth rate. The reproductive rate (0.74 foals/year) was similar to other zebra populations (Smuts 1976, Grange *et al*. 2004) and the survival of the young (0.37) was very close to that reported in Serengeti (0.39, Grange *et al*. 2004). In this population, therefore, the reproductive rate was not a limiting factor. The major contribution of survival of young age classes to the low population growth rate compared to the stable population in Serengeti led the mean generation time of the population to increase markedly, which indicates a much lower renewal rate of individuals over years.

In this declining zebra population, the low survival rates of young age classes were not compensated by high reproductive rates, which led the life cycle to slow down, and consequently, the population to decline. Such a demographic pattern, involving low survival (especially in pre-reproductive age-classes) not compensated by an increase in reproductive output, induces a negative population growth rate associated with a slower life cycle, and seems to be a characteristic feature of populations of large herbivores facing high predation. For instance, Nilsen *et al*. (2009) showed that generation time was longer in declining roe deer populations. Low survival rates in females have also been reported in woodland caribou, *Rangifer tarandus* (Wittmer *et al*. 2005) and bighorn sheep (Festa-Bianchet *et al*. 2006) facing cougar predation, and they led these declining populations to exhibit longer generation times. However, this demographic pattern did not occur in a heavily hunted population of wild boar for which the life cycle was accelerated thanks to an earlier reproduction (Servanty *et al*. 2011). With first reproduction around 3 years of age, a gestation length of over a year (Smuts 1976) and only one foal per reproductive event, plains zebras cannot compensate for low survival in young females, and their populations decline under heavy predation.

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Section B

Variations au niveau individuel des réponses à la prédation

Chapitre III

On the differential foraging costs of vigilance between the sexes: the case of a monomorphic mammal, the plains zebra

On the differential foraging costs of vigilance between the sexes: the case of a monomorphic mammal, the plains zebra

Submitted to Behavioural Ecology

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ABSTRACT

Because prey commonly have to trade off between allocating time to forage and detect predators, vigilance is a costly activity. Although these costs have been studied extensively, differences between the sexes have seldom been explored. We investigated this aspect in the plains zebras (*Equus quagga*), a monomorphic species with strong constraints on feeding time, within a wild population which experiences heavy predation. We disentangled factors affecting each side of the trade-off (vigilance, bite rate). Individuals limited costs through multi-tasking, using low cost vigilance. The non-linear relationship between vigilance and bite rate showed that the apparent costs in terms of foraging increased sharply when individuals invested more time in vigilance. Males were more vigilant than females, and for a same level of vigilance (when time spent vigilant was long), they took fewer bites. Their bite rates were consequently reduced to such low levels that intake is likely to have been reduced too. The sexes differed in their responses to variable proxies of predation risk: time spent vigilant decreased with distance to cover in females, and increased with grass height in males; lactating females tended to allocate less time to vigilance than non-lactating ones and young males were less vigilant than stallions or bachelors. We discuss our results on sex-dependent costs of vigilance for foraging in the light of previous studies on equids of the size of zebras and conclude that the main drivers of the differences between the sexes are linked both to the perception of predation risk and to reproduction.

Keywords

Anti-predator behavior; Group living; Herbivores; Sex effect; Vigilance; Visibility; Zebra

Introduction

Prey commonly have to trade-off time between feeding and avoiding predators (Brown 1999; Krause and Ruxton 2002). Vigilance then has costs, as the time spent detecting predators reduces the time available for feeding, including the time needed for locating food patches. The costs are particularly important when the prey have strong time constraints on foraging (e.g. Ale and Brown 2007 or Beauchamp 2009 for a review). The McNamara-Houston model (1992) shows how crucial it is to understand that when animals are limited by time in their access to food, any trade-off ultimately affects their food intake rate. While situations where vigilance activity is constrained have been found in group-forming prey species during the last decades (presence of competitors, high predation risk or poor foraging patches), the occurrences and importance of sex differences in costs of vigilance are less well understood.

Differences in the costs of vigilance can be expected between sexes as they may differ in the time allocated to vigilance, or in their rate of food intake. Pays and Jarman (2008) identified several mechanisms explaining differences in vigilance activity between the sexes and predicted different patterns for the sexes. There are two main hypotheses relevant for gregarious species. The first suggests that direct interference between males (e.g. for territoriality or for access to females) requires them to monitor the presence and activity of potential rivals continuously (Baldellou and Henzi 1992) in particular if an oestrous female is present. Secondly, in mammals, including herbivores, females are particularly constrained in their time allocation, as their nutrient requirements and food intake increase strongly during lactation (by a factor of > 2, Speakman 2008; for sheep see Penning et al. 1995 and Boulot et al. 1987 for domestic horses). We can therefore predict different absolute energy requirements: females would need more time to forage and between-sexes differences in diet selectivity could trigger differences in foraging bout length (Clutton-Brock et al. 1982).

One promising way to study the costs of vigilance is to investigate the relationship between the proportion of time spent in vigilance and food intake (Cowlishaw et al. 2004). Understanding the way in which vigilance affects intake rates is needed to identify the constraints acting on the trade-off between them. It has been reported that food intake decreases when vigilance increases both in mammals and birds (Fortin et al. 2004; Baker et al. 2011) through a non-linear relationship (Cowlishaw et al. 2004). Such a foraging cost of vigilance can be unambiguously identified when vigilance is exclusive (i.e. when the vigilant act leads to disruption of the ingestion process) and when a high rate of vigilance triggers a decline in the rate of food intake. For instance, such a scenario can be expected in herbivores living in a risky environment, when prey need high quality information to detect potential predators and thus need to stop chewing, as this may hide noises made by predators. Nonetheless, little is known about the differential foraging costs of vigilance between sexes in such contexts of strong constraints.

Some prey species have the ability to share a predator-detection posture with another activity. Indeed, they can multitask, reallocating time while foraging to scanning their surroundings, scrounging, monitoring other group members to limit interference from other individuals for access to food or to maintain spatio-temporal cohesion of the group (Raveh et al. 2011). It is for instance the case for birds handling seeds (Popp 1988; Baker et al. 2011) and mammals chewing food with their heads up (Fortin et al. 2004; Blanchard and Fritz 2007; Makowska and Kramer 2007). Although theory has shown that herbivores could spend as much as 50% of their time scanning without reducing their food intake (through vigilance while chewing or swallowing, Illius and FitzGibbon 1994), multitasking has been proved empirically not to be completely cost-free: bison *Bison bison* and elk *Cervus canadensis* should have been able to maintain their rate of food intake while scanning, but, their bite rate nonetheless declined when they were more vigilant (Fortin et al. 2004). The ability to use this low cost vigilance (vigilance while feeding) could nonetheless be particularly advantageous in herbivores, as they generally forage in food-saturated environments, so short term food intake is limited by chewing and swallowing rates rather than by the encounter rate of food (Spalinger and Hobbs 1992). In a multitasking context, it is more difficult to determine how much prey trade for vigilance when they scan their environment while feeding, as (1) individuals may sustain an acceptable intake rate and (2) food characteristics are expected to influence both bite rate and the amount of spare time available for low cost vigilance.

In African savanna ecosystems, large mammalian herbivores forage in landscapes with high resource heterogeneity (Venter et al. 2003; Gaylard et al. 2003). Responses of prey to heterogeneity on their food resources are strongly affected by large carnivores, through direct lethal effects (Sinclair et al. 2003; Grange et al. 2004) and indirect behavioral effects (Valeix et al. 2009a, b; Thaker et al. 2010). We studied a population of wild zebras (*Equus quagga)*, an extremely social and preferred prey of lions (Hayward and Kerley 2005). Zebras are not sexually dimorphic in their body-size, and experience high feeding constraints. Equids have a high intake feeding strategy (Duncan et al. 1990) which leads them to spend over 50% of the 24 hrs feeding; about 25% of their time is spent resting, so a maximum of 25% remains for all the other activities including vigilance, unless they multitask. For instance, female Plains zebras feed for 69% of their time in the dry season in Kenya, and 57% of it in the wet season (Gakahu 1982). By comparison, other medium-sized herbivores are less constrained as they almost always spend less than 50% of the time feeding (Owen-Smith 1988, Fig. 6.4 for data on zebras and several other species).

We investigated how the sex of the animals, and their social and reproductive status, age, group size and proxies of predation risk (visibility while foraging through grass height and distance to cover), affect the costs of vigilance indicated by the relationship between their investment in vigilance and feeding (bites per minute). As individuals can potentially reduce the high cost of predator detection through different postures, we distinguished the two forms of vigilance (high versus low cost) according to whether individuals interrupted their ingestion process or not while scanning their environment (as defined in Blanchard and Fritz 2007). The bite rate can provide useful information on food intake, but only if it falls to low levels. We use detailed work on horses to interpret the results on the zebras: in horses of the zebra size, average bite rates are always above 15 bites/min, and this rate increases as bite size declines (Fleurance et al. 2009, Fig. 2), allowing the animals to maintain high intake rates across a wide variety of swards. Very low bite rates (fewer than 15 bites/min) indicate low intakes; we assume that this is true for zebras too.

We tested for several forms of relationship between vigilance and bite rate to detect whether an expected decrease of feeding with vigilance rate was characterized by a linear or a non-linear process. As zebras experience heavy predation in Hwange (see Chapter II), as in other ecosystems (Grange and Duncan 2006) and spend 14 to 16 hours feeding per day (Gakahu 1982), we expected strong constraints on the time available for vigilance. We predicted that they should reduce the costs of vigilance by multitasking i.e. by using mainly low cost vigilance (being vigilant while feeding). We expected that the zebras would increase their vigilance during the daytime (i.e. when observations occurred), when their perception of predation risk increased i.e. when close to cover (as lions generally remain in cover during the daytime) and when grass height increased (thus decreasing visibility). As zebras are not sexually dimorphic in body-size, there is no clear *a priori* functional reason to expect variation of vigilance costs between the sexes, regarding differential investment in vigilance and/or foraging. However, concerning within-sex variation of vigilance, lactating female zebras should spend more time feeding than other females, therefore being less vigilant. Males with harems and bachelors trying to access females should spend more time being vigilant than other males, as they need to scan both for predators and potential competitors.

Material and Methods

Study area and animals

The fieldwork was conducted in the Main Camp area of Hwange National Park (HNP) in South-Western Zimbabwe (19°00’S, 26°30’E) from March to July 2009. The study site is an open grassland area of ca. 64 ha enclosed by *Acacia*/*Combretum* bushes, one of the plant communities characteristic of the mixed bushed grassland of the eastern Kalahari sands region (Rogers 1993). Long-term mean annual rainfall is around 606 mm, which mainly occurs during a rainy season from the end of October to the end of April (Chamaillé-Jammes et al. 2007).

Plains zebras are a gregarious species and form non-territorial harems consisting of a stallion, one or more female(s) (generally not more than five) and their foals (Klingel 1969). Young zebras disperse from the age of c. 2 years: young females join existing harems, and young males usually form bachelor groups.

Zebras can be identified individually from their unique strip patterns. The zebra population of Main Camp has been followed since July 2004, with sessions conducted every six months. A database was built, including all sightings with individual characteristics: age class, reproductive status and dominance behaviors, family structures, and individual photos (both sides of each zebra). Information on individuals were gathered each session and entered in the database. In this analysis, we determined for each individual the sex, age class (foal and yearling versus subadult and young adult versus prime and senescent), reproductive status in males (young versus bachelor versus stallion), rank in the social hierarchy in females of the same group (we estimated the rank of a female by observing dyadic interactions between her and the mares of a same group and noting the number of mares who dominated her) and assessed visually whether adult females were pregnant (we defined pregnant females as females with obvious signs of late pregnancy: large abdominal profile and/or swollen udders) and/or lactating (yes versus no).

The main predators of zebras in the study area are lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (Loveridge et al. 2007; Drouet-Hoguet 2007).

Behavioral data

Behavioral data were collected by videotaping (video camera: Sony DCR-SR30, 20× optical) from vehicles, respecting a minimal distance of 100m between the focal group and the observer to minimize disturbance. Animals were chosen at random for a 5-min focal during the daytime. We considered groups whose predominant activity was foraging and which did not move far during the recording, ensuring that group size and composition did not change during the video sequence. Spatial groups were identified on the basis of a maximal separation between adjacent members of 50m, and on the maintenance of social and spatial cohesion of the group members during all focal sampling (as in Frid 1997 for other mammals). There were no ambiguities in defining a group using these criteria as inter-individual distances were very small. Group size was therefore taken as being equal to the size of the spatial group.

Distance to cover ($D \leq 25$, $25 < D \leq 100$, $D > 100$m) was estimated while filming. It is commonly used as a proxy for predation risk (Lima 1990; Burger et al. 2000; Blumstein et al. 2003), but its role (i.e. obstructive or protective) is still ambiguous for prey, and depends on many factors concerning both the predator and the prey. Expectations on the effect of distance to cover on individual vigilance are therefore not clear. However, as zebras use open areas, and as its main predator, the lion, spends the daytime in the cover, we can assume that zebras perceive proximity to cover as risky.

Visibility around foraging individuals provides direct information on their visual obstruction (Whittingham et al. 2004). For example, it has been found in socially foraging birds that vigilance increased with a decrease in visibility around prey (Guillemain et al. 2001). We estimated the grass height of the patch in which the focal individual was foraging. We considered grass to be short when it was not above the focal zebra’s hooves and tall when grass height reached the tibia, which is above their eyes when feeding. In tall grass, visibility is strongly reduced when feeding in the herb layer.

We considered that an animal was vigilant when it raised its head above the horizontal, scanning its surroundings, without moving its feet. No ambiguities were encountered in distinguishing a vigilant from a non-vigilant animal. We also differentiated the time during which individuals were vigilant while chewing (low cost vigilance) or not chewing (high cost vigilance). We extracted from each sequence the total time spent in vigilance and in low and high cost vigilance, the total number of vigilant acts, the total number of steps and, when possible, the total number of bites taken by the individual. Measuring intake rates in lion infested bush was not feasible, so we used bite rates as an indicator of intake rates (see Introduction L 118-122).

Individual zebras were identified in the field, and from the video-tapes after the focal was finished. In total, 162 focals were recorded (110 males and 52 females), corresponding to 47 zebras (20 males and 27 females).

Data analyses

Between sex variation in vigilance

To examine whether sex affected the time spent in vigilance, we ran a linear mixed-effects model with the total time spent vigilant as the dependent variable, and sex, age of the individual, distance to cover, grass height, group size and interactions between these factors as independent variables; individual identity was included as a random factor (model 1, Table 1). We used the same procedure to examine whether sex affected the total time spent in low cost vigilance (model 2, Table 1).

Prey can adjust their vigilance by varying the duration, or the frequency of scans or both (Carter et al. 2009; Périquet et al. 2010). For a given allocation of time spent in vigilance, an individual has the opportunity to make short and frequent scans or long, infrequent scans. The same analysis was therefore performed on the total number of vigilant acts done during 5-min focal (model 3, Table 1).

Some individuals used only low cost vigilance (and not high cost vigilance) whereas other used both. We therefore investigated which factors affected the probability of employing the costly posture of vigilance (0: no high cost vigilance and 1: presence of high cost vigilance in the 5-min video sequence). We ran a generalized linear mixed-effects model with the Laplace procedure (binomial, link: Logit) including the same independent variables and random factors listed in the previous procedure (model 4, Table 1).

Between sex variation in foraging costs of vigilance

To investigate sex effect on vigilance costs on foraging, we derived all possible candidate models examining different forms of relationships between bite rate and vigilance. We used mathematical transformations of the dependent (bite rate) and/or independent (vigilance) variable to determine which model fitted our observations best, including the linear and several forms of non-linear relationships. Table 2 presents candidate models with the bite rate as the dependent variable either non-transformed (models 5-9) or log-transformed (models 10-12) and the total time spent in vigilance as the independent variable non-transformed, log-transformed or arcsine-square root- transformed, with or without the quadratic term of the log-transformed total time spent vigilant.

We controlled for the total number of steps made by the individuals, group size, distance to cover, grass height and age. Potential differences in vigilance costs between the two sexes were tested by including sex, and interactions between vigilance and sex as independent variables. We used a linear mixed-effects model approach with individual identity as a random factor. Akaike's criterion (AIC) and the corrected criterion (AICc) for each candidate model were calculated, including the null model (Burnham and Anderson 2002). The best model had the lowest AICc and the highest weight (ω_i) indicating the probability of being the best among all the model candidates. We also calculated the pseudo R^2 of the two best candidate models to help us determine whether log-transforming the dependent variable (bite rate) improved the model or not.

Since the difference in the strength of the relationship between bite rate and vigilance between the two sexes could come from morphological, physiological or environmental constraints dependent on (or exclusive to) each sex, affecting either vigilance or bite rate or both, we analyzed the effects acting on, first, vigilance and second, bite rate in each sex separately.

Factors affecting the variation of vigilance and bite rate within the sexes

We tested the effect of reproductive status of male on their total time spent in vigilance and frequency of vigilant acts, controlling for the effects of group size, grass height and distance to cover (models 13-14, Table 1). In females, we first tested if hierarchical position in the group influenced vigilance (models 15-16, Table 1). We then restricted the analyses to adult females, and tested first for the effect of being pregnant (models 17-18, Table 1) and secondly the effect of lactation (models 19-20, Table 1). We also controlled for the effects of group size, grass height and distance to cover. We computed complete linear mixed-effect models including all independent variables cited above and their interactions as fixed factors, with individual identity as a random factor for all cases. In a final step, we repeated on the bite rate of individuals, the analysis performed by sex on vigilance (models 21-24, Table 1).

ID Model	Sex class used in the analysis	Dependent variable	Independent variables
1	Both	Log(Dur Total Vigilance)	Sex + Age + Group Size + Distance to Cover + Grass Height + Sex×Age + Sex×Group Size + Age×Group Size
2		Log(Dur Low Cost Vigilance)	
3		Log(Frequency Vigilant acts)	
4		Probability High Cost Vigilance	
13	Male	Log(Dur Total Vigilance)	Reproductive Status + Group Size + Distance to Cover + Grass Height + Reproductive Status×Group Size
14		Log(Frequency Vigilant Acts)	
15	Female	Log(Dur Total Vigilance)	Hierarchy + Group Size + Distance to Cover + Grass Height + Hierarchy×Group Size
16		Log(Frequency Vigilant Acts)	
17	Adult Female	Log(Dur Total Vigilance)	Pregnancy + Group Size + Distance to Cover + Grass Height + Pregnancy×Group Size
18		Log(Frequency Vigilant Acts)	
19	Adult Female	Log(Dur Total Vigilance)	Lactation + Group Size + Distance to Cover + Grass Height + Lactation×Group Size
20		Log(Frequency Vigilant Acts)	
21	Male	Log(Bite rate)	Reproductive Status + Group Size + Distance to Cover + Grass Height + Reproductive Status×Group Size
22	Female	Log(Bite rate)	Hierarchy + Group Size + Distance to Cover + Grass Height + Hierarchy×Group Size
23	Adult Female	Log(Bite rate)	Pregnancy + Group Size + Distance to Cover + Grass Height + Pregnancy×Group Size
24			Lactation + Group Size + Distance to Cover + Grass Height + Lactation×Group Size

Table 1: Summary of variables included in the different linear mixed effects models including individual identity as a random factor.
Log(Dur Total Vigilance), Log(Dur Low Cost Vigilance) and Log(Frequency Vigilant acts) are respectively the Log-transformation of the total and the low cost time spent in vigilance and the number of vigilant acts performed during 5-min focal. Probability high cost vigilance is the probability to exhibit at least one high cost vigilant acts during 5-min focal. Step number is the number of step during 5-min focal. Sex (male *versus* female), age class (foal and yearling *versus* subadult and young adult *versus* prime and senescent), reproductive status in males (young *versus* bachelor *versus* stallion, hierarchy rank in females (four ranks from dominant to dominate), whether adult females were pregnant (yes *versus* no) and lactating (yes *versus* no), distance to cover ($D \leq 25$, $25 < D \leq 100$, $D > 100$m) and grass height (short versus tall) were categorical variables.

Factors affecting the variation of vigilance and bite rate within the sexes

We tested the effect of reproductive status of male on their total time spent in vigilance and frequency of vigilant acts, controlling for the effects of group size, grass height and distance to cover (models 13-14, Table 1). In females, we first tested if hierarchical position in the group influenced vigilance (models 15-16, Table 1). We then restricted the analyses to adult females, and tested first for the effect of being pregnant (models 17-18, Table 1) and secondly the effect of lactation (models 19-20, Table 1). We also controlled for the effects of group size, grass height and distance to cover. We computed complete linear mixed-effect models including all independent variables cited above and their interactions as fixed factors, with individual identity as a random factor for all cases. In a final step, we repeated on the bite rate of individuals, the analysis performed by sex on vigilance (models 21-24, Table 1).

To achieve normality and homoscedasticity in all statistical procedures described above, we log-transformed the total time spent in vigilance, the total number of vigilant acts and the bite rate of individuals (the transformation was chosen on the basis of the previous analysis, investigating the form of the relationship between bite rate and vigilance).

The large number of continuous and categorical variables decreased the degrees of freedom in our statistical procedures, so, in each model, we included only two-way interactions which were biologically relevant and interpretable in terms of mechanisms influencing vigilance costs.

Statistical analyses were performed using R 2.12.0 (R Development Core Team, 2010).

Results

Between sex variation in vigilance

The zebras spent around 10% of their feeding time being vigilant, with a high variability between samples (range: 0 to 92% of the time). Vigilance was composed mainly of low cost vigilance: 71% of the individuals which were vigilant during the samples were engaged in low cost vigilant acts only and 79% of the total time spent vigilant by individuals was made up of low cost vigilance. Controlling for the effect of distance to cover, grass height, group size, age class and their interactions, the sexes differed in their frequency of vigilant acts ($F_{1,41}$ = 5.199, P = 0.028) and tended to differ in their time spent in vigilance ($F_{1,41}$ = 3.582, P = 0.066). Males were more vigilant than females according to the coefficient (± SE) derived for males for the frequency of vigilant acts (0.115 ± 0.050) and their time spent in vigilance (0.173 ± 0.090) when females were used as the reference.

Controlling for the factors cited above, the sexes tended to differ in their time spent in low cost vigilance ($F_{1,41}$ = 3.384, P = 0.073). According to the coefficient (± SE) derived for males (0.160 ± 0.087) when females were used as the reference, males tended to spend more time in low cost vigilance than did females. However, females and males did not differ in their probability of performing a high-cost vigilance posture during the 5-min video sequences (χ^2_2 = 0.005, P = 0.94).

Between sex variation in foraging costs of vigilance

Controlling for the effect of group size, number of steps, distance to cover, grass height and age of the individual, table 2 shows that the best candidate models to explain the variation of bite rate with vigilance were the model 8b and 11b respectively. These models are similar in their independent variables as they both included the log-transformed duration of the total time spent in vigilance, the quadratic term of this variable and the interactions of these variables with sex. The pseudo-R square values for models 8b and 11b show that the best model was ultimately 11b, which includes the log-transformed bite rate. Finally, the log-transformation of the total time spent in vigilance gave a better fit than the classical arcsine-square root-transformation of the proportion of time spent in vigilance. To summarize, the relationship between bite rate and vigilance was best characterized by a log-log link including a polynomial function of the log-transformed total time spent in vigilance.

Table 3 shows which factors influenced the strength of the relationship between bite rate and vigilance. Controlling for the effect of group size, number of steps, distance to cover, grass height, age of the individual and two way interactions between these factors, the log-transformed bite rate decreased in a curvilinear way with increasing time spent vigilant (log-transformed). Moreover the strength of the relationship between the log-transformed time spent vigilant and bite rate differed between the two sexes. As a consequence of the significant effect of the interaction between sex of the individual and the quadratic term of the log-transformation of the total time spent vigilant, females took more bites than males for the same level of vigilance, but only at high levels of vigilance (> c. 30 seconds, i.e. >10% of the time, Fig. 1).

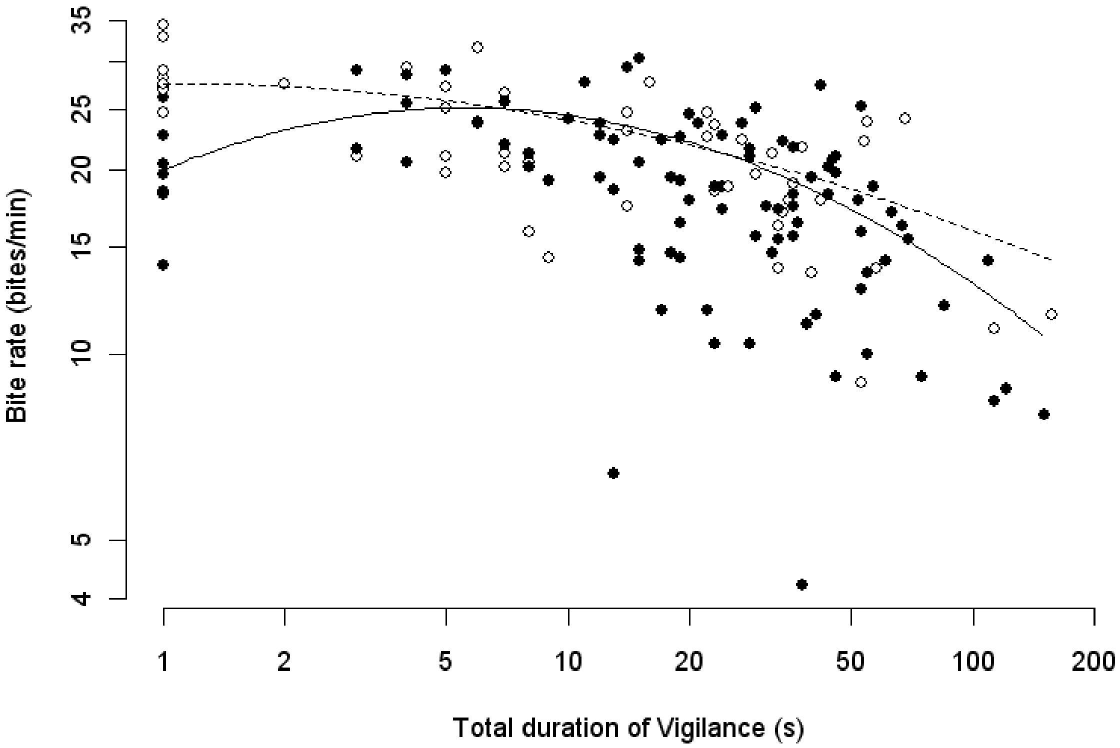

Figure 1: Relationship between the log-transformed total time spent in vigilance and the bite rate in male (black dots, full line) and female (white dots, dashed line) zebras during 5-min focal. Fitted curves are derived from the model in the table 1 assessed with mean values of group size and step numbers.

Table 2: Selection of the best model explaining the relationship between bite rate and time spent vigilant.

ID Model	Dependent Variable	Independent Variables	LogLik	k	AIC	AICc	ΔAICc	ω_i	Pseudo R^2
Null	Bite rate	*(f)*	-688.44	12	1400.89	1403.24	77.96	0.00	
5	Bite rate	Dur Total Vigilance + *(f)* + Dur Total Vigilance × Sex + Dur Total Vigilance × Group Size + Dur Total Vigilance × Step Number	-654.62	16	1341.24	1345.46	20.18	0.00	
6	Bite rate	Dur Total Vigilance + (Dur Total Vigilance)^2 + *(f)* + Dur Total Vigilance × Sex + Dur Total Vigilance × Group Size + Dur Total Vigilance × Step Number	-649.99	17	1333.99	1338.77	13.50	0.00	
7	Bite rate	Log(Dur Total Vigilance) + *(f)* + Log(Dur Total Vigilance) × Sex + Log(Dur Total Vigilance) × Group Size + Log(Dur Total Vigilance) × Step Number	-652.29	16	1336.58	1340.80	15.52	0.00	
8	Bite rate	Log(Dur Total Vigilance) + (Log(Dur Total Vigilance))^2 + *(f)* + Log(Dur Total Vigilance) × Sex + Log(Dur Total Vigilance) × Group Size + Log(Dur Total Vigilance) × Step Number	-645.46	17	1324.92	1329.70	4.43	0.10	
8b	Bite rate	Log(Dur Total Vigilance) + (Log(Dur Total Vigilance))^2 + *(f)* + Log(Dur Total Vigilance) × Sex + (Log(Dur Total Vigilance))^2 × Sex + Log(Dur Total Vigilance) × Group Size + Log(Dur Total Vigilance) × Step Number	-641.94	18	1319.89	1325.28	0.00	0.88	0.52
9	Bite rate	Asin(Prop Total Vigilance)$^{0.5}$ + *(f)* + Asin(Prop Total Vigilance)$^{0.5}$ × Sex + Asin(Prop Total Vigilance)$^{0.5}$ × Group Size + Asin(Prop Total Vigilance)$^{0.5}$ × Step Number	-648.11	16	1328.24	1332.46	7.18	0.02	
Null	Log(Bite rate)	*(f)*	85.91	12	-147.82	-145.47	77.84	0.00	

Table 2 (continued)

10	Log(Bite rate)	Log(Dur Total Vigilance) + *(f)* + Log(Dur Total Vigilance) × Sex + Log(Dur Total Vigilance) × Group Size + Log(Dur Total Vigilance) × Step Number	119.24	16	-206.49	-202.27	21.04	0.00	
11	Log(Bite rate)	Log(Dur Total Vigilance) + (Log(Dur Total Vigilance))^2 + *(f)* + Log(Dur Total Vigilance) × Sex + Log(Dur Total Vigilance) × Group Size + Log(Dur Total Vigilance) × Step Number	128.69	17	-223.39	-218.61	4.70	0.08	
11b	Log(Bite rate)	Log(Dur Total Vigilance) + (Log(Dur Total Vigilance))^2 + *(f)* + Log(Dur Total Vigilance) × Sex + (Log(Dur Total Vigilance))^2 × Sex + Log(Dur Total Vigilance) × Group Size + Log(Dur Total Vigilance) × Step Number	131.97	18	-227.94	-223.31	0.00	0.89	0.57
12	Log(Bite rate)	Asin(Prop Total Vigilance)$^{0.5}$ + *(f)* + Asin(Prop Total Vigilance)$^{0.5}$ × Sex + Asin(Prop Total Vigilance)$^{0.5}$ × Group Size + Asin(Prop Total Vigilance)$^{0.5}$ × Step Number	126.32	16	-220.64	-216.42	6.89	0.03	

Akaike's criterion (AIC) and the corrected criterion (AICc) for each candidate model explaining the variation of the relationship between bite rate and the time spent in vigilance testing for linear and non-linear links. Dur Total Vigilance is the total time and Prop Total vigilance is the proportion of time spent in vigilance during the 5min focal. The best model (in bold) has the lowest AICc. LogLik is the Loglikelihood, k is the number of estimated parameters. The best model with the lowest AICc is in bold. ΔAICc is the difference between that model's AICc; ω_i is the weight of the model indicating the probability that a given model is the best among the model candidates. *(f)* is an addition of controlling factors including step number, sex, group size, distance to cover, grass height and age. The null models included only *(f)* and the individual identity as a random factor. Pseudo R square of the two best candidate models is given.

Factors affecting the variations of vigilance within the sexes

We investigated the factors influencing the total time spent in vigilance and the frequency of vigilant acts in males and females separately. First, the statistical analyses showed that reproductive status affected the frequency of vigilant acts in males ($F_{2,82}$ = 4.100, P = 0.020). Bachelors and stallions were vigilant once a minute; young males still in their family group only about once every one minute and a half (Fig. 2). Moreover, males foraging in a tall grass patch tended to scan more frequently than in a short grass patch ($F_{1,82}$ = 3.194, P = 0.078, Tall: coef ± SE = 0.091 ± 0.062).

Reproductive status ($F_{2,82}$ = 1.910, P = 0.156), grass height ($F_{1,82}$ = 1.329, P = 0.252), distance to cover ($F_{2,82}$ = 1.791, P = 0.173), group size ($F_{1,82}$ = 0.127, P = 0.722) and the interaction between reproductive status and group size ($F_{2,82}$ = 0.195, P = 0.823) did not affect the time that males spent in vigilance. Moreover, distance to cover ($F_{2,82}$ = 0.380, P = 0.685), group size ($F_{1,82}$ = 0.311, P = 0.579) and the interaction between reproductive status and group size ($F_{2,82}$ = 0.634, P = 0.533) did not affect the frequency of vigilant acts in males.

In females, distance to cover significantly affected the total time spent in vigilance ($F_{2,18}$= 4.076, P = 0.035), with females spending about twice as much of their time vigilant when close to the cover (> 100m versus 0-25 and 26-100 m, Fig. 3). Lactating females tended to be less vigilant (coef ± SE = -1.053 ± 0.463) than others ($F_{1,18}$ = 3.759, P = 0.066).

There were no significant effects of rank on the total time spent vigilant by females ($F_{3,23}$ = 0.360, P = 0.782), or of grass height ($F_{1,18}$ = 2.718, P = 0.117), group size ($F_{1,18}$ = 0.079, P = 0.782), or the interaction between rank and group size ($F_{3,18}$ = 1.667, P = 0.210). In adult females, the duration of vigilance was not affected by pregnancy status either ($F_{1,21}$ = 0.066, P = 0.800), or by the interactions between pregnancy status and group size ($F_{1,18}$ = 0.207, P = 0.655) and between lactation and group size ($F_{1,18}$ = 2.605, P = 0.124). Moreover, rank ($F_{3,23}$ = 0.454, P = 0.717), grass height ($F_{1,18}$ = 1.610, P = 0.221), distance to cover ($F_{2,18}$ = 1.597, P = 0.230), group size ($F_{1,18}$ = 0.148, P = 0.705) and the interaction between rank and group size ($F_{3,18}$ = 1.546, P = 0.237) did not affect the frequency of vigilant acts performed by females. In adult females, the frequency of vigilance was not affected by pregnancy status ($F_{1,21}$ = 0.005, P = 0.944), the interaction between pregnancy status and group size ($F_{1,18}$ = 0.177, P = 0.679), lactation ($F_{1,21}$ =

1.580, P = 0.223) or by the interaction between lactation and group size ($F_{1,18}$ = 2.600, P = 0.124).

Factors	numDF	denDF	F	P	Coef ± SE
(Intercept)	1	90	52734.91	<0.001	2.100 ± 0.058
Log(Dur Total Vigilance)	1	90	84.76	<0.001	0.004 ± 0.092
(Log(Dur Total Vigilance))^2	1	90	16.57	<0.001	-0.061 ± 0.041
Step number	1	90	32.55	<0.001	0.001 ± 0.001
Sex	1	41	6.06	0.018	Male: -0.141 ± 0.058
Group size	1	90	5.46	0.022	0.009 ± 0.005
Distance to cover	2	90	2.15	0.122	
Grass height	1	90	0.01	0.938	
Age	2	41	2.78	0.074	
Log(Total Vigilance) × Sex	1	90	0.58	0.445	Male: 0.269 ± 0.113
(Log(Total Vigilance))^2 × Sex	1	90	5.94	0.018	Male: -0.121 ± 0.053
Log(Total Vigilance) × Group size	1	90	2.35	0.129	
Log(Total Vigilance) × Step number	1	90	6.69	0.011	-0.002 ± 0.001

Table 3: Factors influencing bite rate including the second degree polynomial function of the log-transformed total duration of vigilance (i.e. Log(Dur Total vigilance)^2). Individual identity was included as a random factor. Step number is the number of step during 5-min focal. Sex (*female*, male), age class (*foal and yearling*, subadult and young adult, prime and senescent), distance to cover (*$D \leq 25$*, $25 < D \leq 100$, $D > 100$m) and grass height (*short*, tall) were considered as categorical and level used as the references in the model are italicized in the legends.

Factors affecting the variations of bite rate within the sexes

Bite rates varied between 0 - 35 bites/min. 22% of the bites were below 15 bites/min (i.e. 25 samples of males and 7 of females), and 12% below 12 bites/min (i.e. 15 samples of males and 3 of females).

In males, there was no effect on bite rate of reproductive status ($F_{2,68}$ = 0.652, P = 0.524), grass height ($F_{1,68}$ = 0.337, P = 0.563), distance to cover ($F_{2,68}$ = 0.565, P = 0.571), group size ($F_{1,68}$ = 1.349, P = 0.250) or of the interaction between reproductive status and group size ($F_{2,68}$ = 1.998, P = 0.144). Bite rates in female were not affected by rank ($F_{3,22}$ = 0.435, p = 0.730), grass height ($F_{1,18}$= 1.705, p = 0.208), distance to cover ($F_{2,18}$ = 1.162, p = 0.335), group size ($F_{1,18}$ = 1.530, p = 0.232), or by the interaction between rank and group size ($F_{3,18}$ = 0.359, p = 0.784). In adult females, bite rate was not affected by pregnancy status ($F_{1,20}$ = 0.110, p = 0.744), the interaction between

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pregnancy and group size ($F_{1,18} = 0.289$, $p = 0.598$), lactation ($F_{1,21} = 2.327$, $p = 0.143$) or by the interaction between lactation and group size ($F_{1,21} = 0.695$, $p = 0.415$).

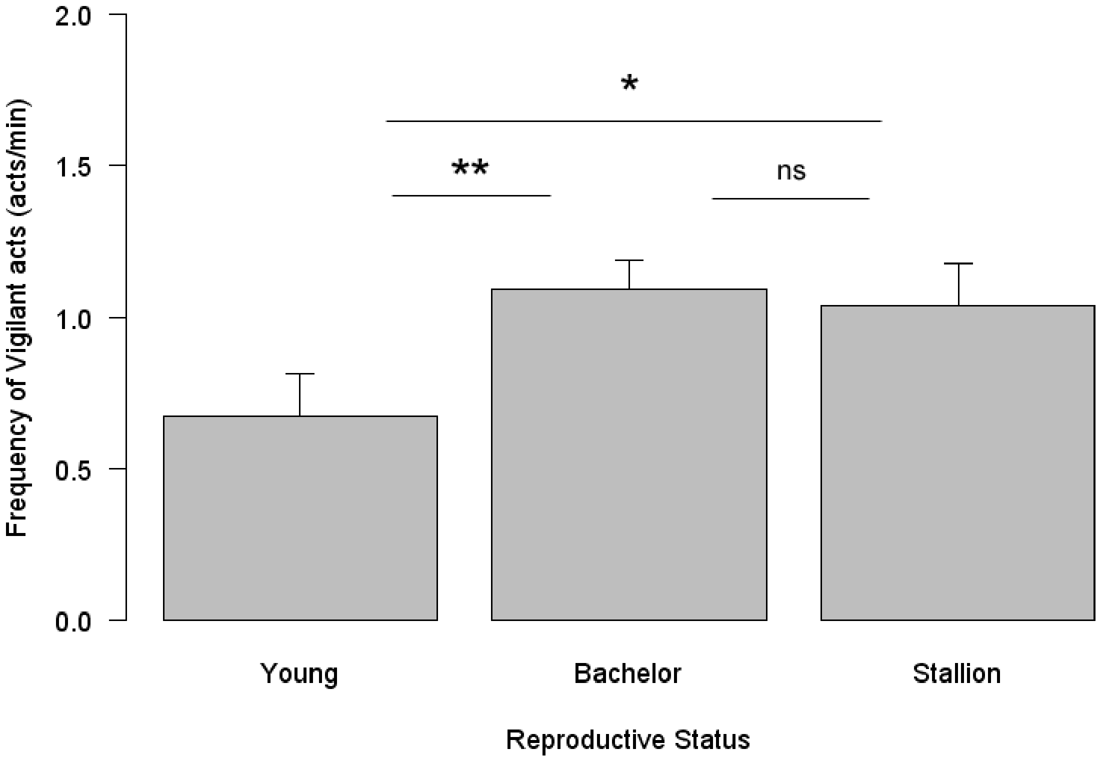

Figure 2: Effect of reproductive status on the frequency of vigilant acts performed during 5-min focal in male zebras. *Error bars* are the standard errors. **,*, ns indicate respectively $P < 0.01$, 0.05 and non significant difference.

Discussion

The relationship between vigilance and bite rate

Although individuals were mainly multi-tasking when they devoted attention to their environment (being vigilant while foraging), which contributes to reducing the costs compared to the higher costs of more intense vigilance, the time spent in low cost vigilance still reduced bite rate (i.e. the number of bite per minute), especially in male zebras when they were vigilant more than 10% of the time. Horses of zebra size foraging without predation in Europe maintain high intake rates across a wide variety of swards (Fleurance et al. 2009, Fig. 3) with average bite rates always above 15 bites/min. In zebras, our results show that bite rates could reach very low values, especially in male zebras (22% of the bites were below 15 bites/min and 12% below 12 bites/min), so food intakes are likely to decline when time spent in vigilance exceeded 13%. The decrease of bite rate with vigilance has been also reported in other herbivorous mammals including bison and elk (Fortin et al. 2004) and birds (Cowlishaw et al. 2004; Baker et al. 2011). However, the non-linear relationship between vigilance and bite rate indicates that the cost associated with vigilance was not proportional to the time spent vigilant in a linear manner. Our results showed that the costs to foraging remained small when zebras spent little time in vigilance (< 15-20 s, i.e. < 5-6% of the total available time) and increased strongly when they invested more time in vigilance. As an individual strategy, if zebras maintain the time devoted to vigilance below this threshold, they will not suffer high costs in terms of foraging.

Zebras, like horses, face a constraint on foraging time and, in our studied population, they have several functional reasons to maximize their intake rate and restrict vigilance during the day to less than 10% of their feeding time: (1) their high intake feeding strategy leads them to spend over 50% of the 24 hrs feeding (Gakahu 1982), (2) they forage on grass, and in HNP, poor soil (Kalahari sands) implies low quality grass, thus a need for greater intake and selection for high quality items, and (3) they are social foragers and inter-individual competition for access to high quality patches is likely (see Giraldeau and Beauchamp 1999; Blanchard et al. 2008), especially in a nutrient poor savanna.

Sex differences in foraging costs of vigilance

Vigilance costs for foraging differed between sexes. Females took more bites than males for low levels of vigilance and the decrease of bite rate with vigilance was higher for males than females for high rates of vigilance (as shown by the interaction between sex and individual investment in time spent vigilant). As a consequence, male bite rates were reduced to such low levels that intake is likely to have been reduced too. In addition, males were more vigilant (low cost vigilance) than females. As zebras are monomorphic, males and females should not differ in their similar absolute energy requirements and predation risk (for a given age and reproductive status). Bite rate and vigilance rate should therefore not differ significantly between males and females. Our results show however that bite rate is a function of both investment in vigilance and sex, and that the impact of the cost of vigilance for foraging is complex, as it is dependent on the gender of the animals. There is no evidence that the relationship between intake and bite rate differs in males and female horses, so the driving forces involved in the mechanism underlying the differential strength of foraging costs of vigilance between the sexes are probably related to differences between the sexes in predator detection or competitor appraisal (i.e. with males being more vigilant than females).

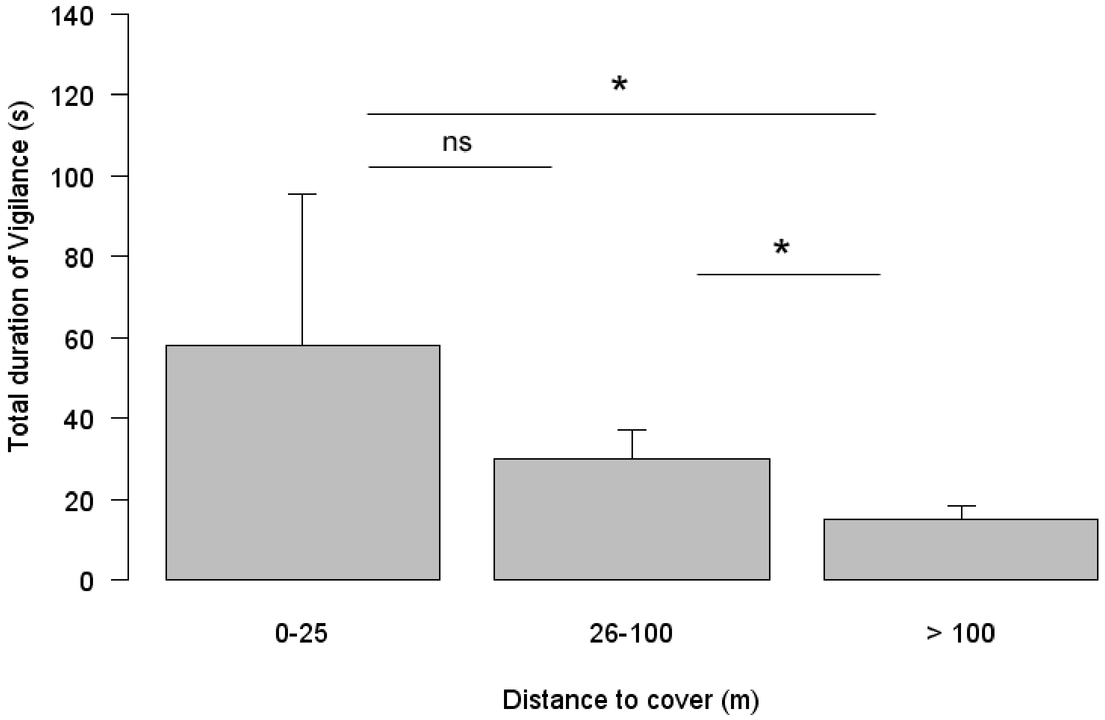

Figure 3: Effect of the distance to cover on the total time spent in vigilance in female zebras during 5-min focal. *Error bars* are the standard errors. *, ns indicate respectively $P < 0.05$ and non significant difference.

Time investment in vigilance

Zebra males spent more time vigilant than females and supported previous results for this species (Burger and Gochfeld 1994), and for other ungulates including African buffalo *Syncerus caffer* (Prins and Iason 1989). However, no differences have been detected in some other mammals including African elephant *Loxodonta africana*, kob *Kobus kob*, impala *Aepyceros melampus* (Burger and Gochfeld 1994), degu *Octodon degus* (Ebensperger et al. 2006) and in wild mixed-species troops of primates (Smith et al. 2004).

Our results highlight sex-dependent factors influencing the time that zebras invested in vigilance. In males, young animals in their family group were less vigilant than bachelors or stallions. This result supports previous observations in elk (Lung and Childress 2006) and in the greater kudus *Tragelaphus strepsiceros* (Pays et al. 2012b). Thus, the hypothesis that males which are protecting their harems and bachelors which are trying to access reproduction should spend more time being vigilant as they need to scan for predators and potential competitors is supported. Arenz and Leger (2000) developed three main reasons to explain why juveniles are less vigilant than adults: (1) juveniles need time to learn certain aspects of their behavior, (2) less vigilance could result from a maturational effect (because of their small size, juveniles may be harder for predators to detect, so juveniles may not need to be as vigilant as adults) and (3) nutritional and energetic requirements differ between juveniles and adults with juveniles constrained to invest in feeding for growth.

Although we did not detect any effect of social rank or pregnancy status on vigilance in females, those lactating tended to be less vigilant than the others. This result differs from Childress and Lung (2003) who showed that female elk with calves are preferentially targeted by wolves *Canis lupis* and are consequently the most vigilant age/sex class. Lactation is the most energetically expensive component of reproduction in mammals, and breeding females are expected to adjust their behavior to compensate for increased nutritional demands. Our results suggest that, as lactating females tend to adjust their time spent in vigilance, they should also tend to increase intake. Adjustment in bite rate in response to increasing energetic demands of reproduction has been experimentally shown using a fertility control agent in free-ranging eastern grey kangaroos (Cripps et al. 2011): reproducing females increased bite rates and thus food intake, when the energetic demands of lactation were highest, although they did not reduce the time spent on vigilance for predators. Our observations also suggest that investing mainly in low cost vigilance might contribute to coping with lactation costs as that posture allows individuals to continue eating while being vigilant (Blanchard and Fritz 2007). Overall, these results on female zebras suggest that energy requirements may be a greater driving force than predation in the trade-off between vigilance and grazing behavior, through the constraint imposed on maintaining high intake rate. However, we believe that this should be confirmed by an analysis on a larger sample size of lactating and non-lactating female zebras.

Differences in the perception of predation risk

Although most of our results do not suggest that predation risk is a major driver of vigilance-intake trade-offs in both zebra males and females, males foraging in a tall grass patch tended to scan more frequently than in a short grass patch and females increased their time spent vigilant when they were foraging close to cover. Thus both sexes still appear to be affected by perception of predation risk, at a local (patch) scale in males and at a broader scale in females. However, even if our results support previous studies in impalas (Pays et al. 2012a) and in socially foraging birds (Guillemain et al. 2001) in which vigilance increased with a decrease of visibility around prey, it still remains possible that the increase in vigilance with taller grass in male zebra is mostly a response to maintain high social vigilance: a reduction in immediate visibility can trigger an increase in vigilance in males, as they need to monitor the presence of other competitors. Furthermore, many studies have recorded a decrease of vigilance when distance to cover increased (Burger et al. 2000; Beauchamp 2010), but others reported that vigilance of prey increased with distance to cover (Carrascal and Alonso 2006; Pays et al. 2009). Such variability seems to be related to many factors, including whether the prey perceived cover as obstructive or protective (Lima 1990). In our case, as zebra tend to select for open areas more intensively in presence of lion (Valeix et al. 2009b), we can safely assume that cover is more likely to be a perceived as obstructive by our studied female zebras.

The population in our study site, is limited by predation (see Chapter II), which would require zebras to be particularly vigilant when predation risk is high. However, distance to cover – a proxy of predation risk - does not seem to influence the time spent vigilant by male zebras. High feeding constraints and the strong competition for access to reproduction might thus limit the possibility for male zebras to invest in anti-predator vigilance, leading to the higher rate of survival of females compared to males in our population (see Chapter II).

Conclusion

The costs of vigilance for foraging appeared sex-dependent, probably as a consequence of different relative contributions of predation risk and reproduction in individual fitness of males and females: we suggest that the primary use of vigilance for male is to monitor conspecifics (triggered by their reproductive status) and that the detection of predators is less important. In female the primary use of vigilance appears to be to detect potential predators. This hypothesis is consistent with the fact that survival rate is higher in females than in male zebras in this population (see Chapter II). In this population of zebras, a social prey highly constrained by food acquisition with males and females differing in their bite rates, individuals of both sexes limited vigilance costs on foraging through multitasking (i.e. using low cost vigilance). However, the high constraints on their foraging time still limited the possibility for individuals to invest much in vigilance. Males were especially constrained as they seem to have higher costs than females when they are more vigilant but females were also highly constrained by the great investment in grazing dictated by the energetic requirements associated to reproduction. The zebras were not often vigilant (around 10% of their time), even though they face a high predation pressure in our study site. The limitation of the population by predators (see Chapter II) might thus reflect the poor behavioral choices made by the zebras due to these high feeding constraints.

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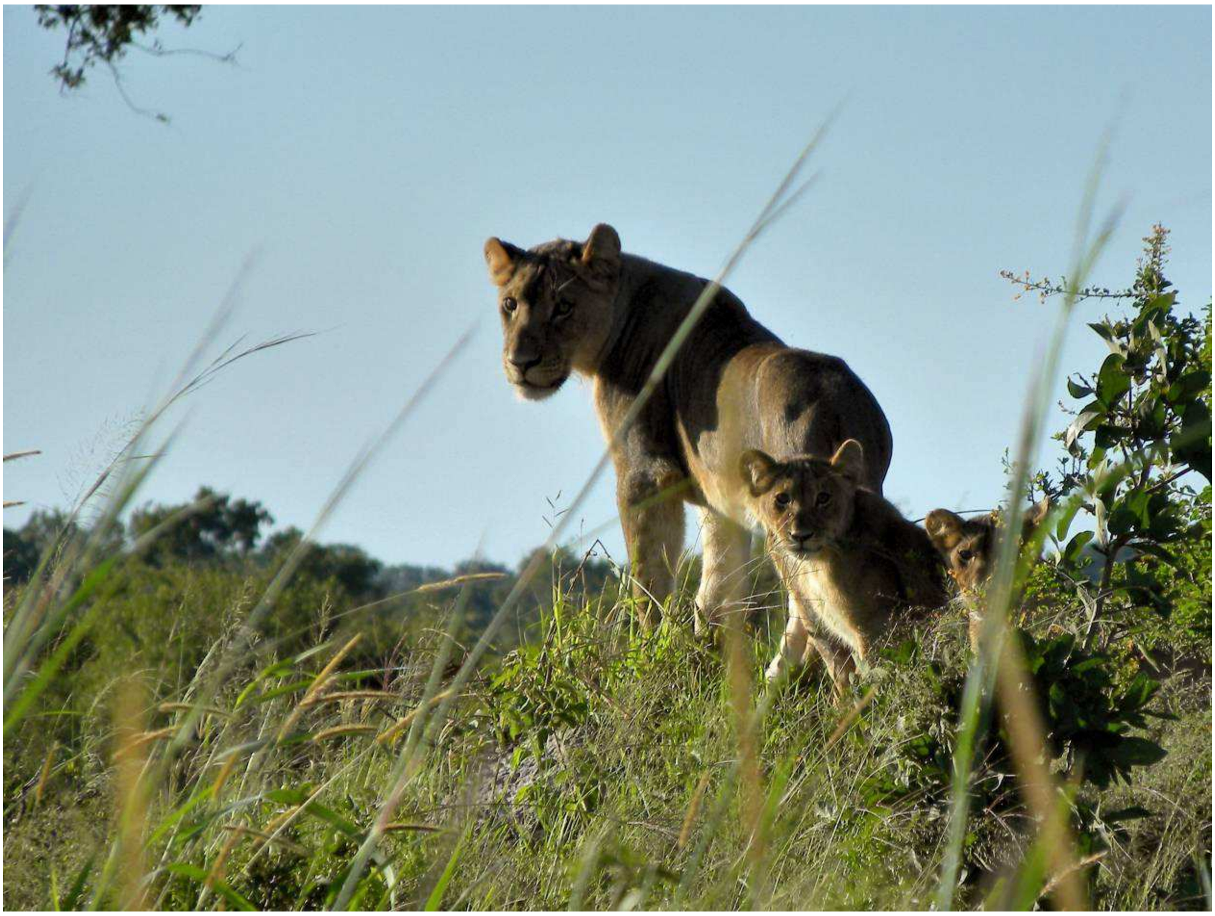
Chapitre IV

What structures vigilance under high predation risk: environment or personality?



What structures vigilance under high predation risk: environment or personality?

In preparation

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INTRODUCTION

It is commonly accepted that prey face a trade-off between spending time for the acquisition of food and for the avoidance of predators. Vigilance as a mechanism for detecting predators has been thoroughly studied: numerous studies have looked at the impact of environmental (e.g distance to cover, Burger et al. 2000, or visibility around individuals, Whittingham et al, 2004) or social factors (e.g group-size effect, Lima 1995) to explain observed differences in vigilance behaviours. However, these studies seldom mention how much of the variance observed is explained by these factors: in his review of the effect of food density on vigilance, Beauchamp (2009) found only 2 studies out of 31 providing R² values of the models explaining variation in vigilance with food density. Vigilance is indeed a very labile behaviour, making any changes in the patterns observed hard to understand and to relate to external factors.

Additionally, consistent individual differences in vigilance could exist and, if so, should be accounted for to disentangle the effects of environmental, social and individual characteristics on vigilance. Recently, within and between individual consistency in behaviour across time and contexts have been shown to be more common than previously thought (Sih et al. 2004; Bell 2007), and have led to assume that personalities or temperaments may be found in animals. Personality has been shown to possibly vary with age and sex (English et al. 2010), and to shape a wide range of behaviours from aggression (Kralj-Fiser et al. 2007) and exploratory behaviour (Quinn & Cresswell 2005) to courtship (Forstmeier & Birkhead 2004) . In a review, Bell and his collaborators (2009) found that around 35% of the variation in behaviour between individuals was due to consistent individual differences. Not taking account of these variations could thus considerably undermine our understanding of how external factors can affect behaviour of individuals. In particular, only few studies have looked at the effect of personality on antipredator behaviour, and even less on vigilance, but they found that vigilance behaviour was repeatable: Blumstein et al. (2004) found that the repeatability of vigilance behaviour within individuals was 0.29 and Couchoux and Cresswell (2012) found a repeatability of 0.21. This raises the question of how risk is perceived by individuals: is risk more intrinsic to individuals, with some of them always more vigilant than others, or is it more associated with environmental cues?

In social species forming groups, the group itself might structure the behaviour of its individuals. Indeed, the animal social network structure can be affected by the personality types of its group members (Pike et al. 2008). The interaction between personality of an individual and the social network he lives in, while being complex, can help to explain biological patterns that occur at the group level (Krause et al. 2010), like group-decision making (Conradt & Roper 2003; Magnhagen & Bunnefeld 2009). Individuals have also been shown to generally assort phenotypically in social groups (Krause & Ruxton 2002). Associations between individuals with similar personality could induce differences in responses between groups, and could thus explain why individuals from different groups show differences in behaviour.

Plains zebras (*Equus quagga*) is a highly social species forming harems of several individuals with tight bonds between them. Predation by lions has been suggested to have strong effects on zebra population dynamics in Hwange National Park (see Chapter II), our study area. We thus expect zebras to respond strongly to predation risk by lions, and to adopt effective antipredator strategies to avoid them. In particular, vigilance behaviour in zebras has been shown to be affected by the presence of lions (Periquet et al. 2012), and is thus of interest. Indeed, investment in vigilance could differ between individuals and/or groups and might be repeatable at both or at one of these levels.

In this study, we performed a playback experiment, contrasting conditions of unknown predation risk with conditions of high perceived predation risk on different plains zebra groups composed of known individuals. We tested for the importance of environmental and social factors in vigilance behaviour in these two contrasting contexts. We tried to better understand how vigilance is structured between individuals and between groups, how the perceived risk of predation can affect this structure and also tried to better understand repeatability in behavioural patterns both at the individual and the group level.

MATERIAL AND METHODS

Study site and animals

Fieldwork was conducted in the Main Camp area of Hwange National Park (HNP), in western Zimbabwe, a wooded savanna on Kalahari sands with open grassy patches (Rogers 1993). The year is separated in a dry and a wet season, with a mean annual rainfall of 606 mm.

We conducted the experiment during the wet season of 2011, from January to April. Plains zebra (*Equus quagga*) density is estimated to be around (mean ± SD) 0.80 ± 0.43 individuals/km² in the study area (Chamaillé-Jammes et al. 2009). Zebras have a particular social system, with harems and bachelor groups: harems are formed with 1 stallion, 1 up to 5 females, with or without foals. These groups are known to be stable over months to years (Rubenstein & Hack 2004) and this is consistent with our observations from the field as no individual was seen in two different groups during the observations reported here. Bachelor groups are made up of males with no females. We choose not to work with bachelor groups as bonds between bachelors are loose, and they often change groups.

Since 2004, the sub-population of zebras in the Main Camp area of HNP has been individually monitored, with sessions conducted every 6 months. More than 20 harems, with the individuals which compose them, were therefore known, and easily identified on the field. Playback experiments were thus conducted on individually identified zebras in known harems.

Playbacks

In HNP, the predation pressure on zebras is very high (see Chapter II), particularly from lions (*Panthera leo*, Loveridge et al. 2007). We thus chose to look at the reaction of zebras to lion roars, simulating a high predation risk. The experiment was performed early in the morning between 6:00 and 8:30, when lions are still active (Schaller 1972). When a known harem was found, we made sure the animals were behaving normally before beginning the recording of the behavioural sequence. We videotaped (video camera: Sony DCR-SR30 (Sony Corporation, Tokyo, Japan), 20× optical zoom) all members of the focal harem, making sure all individuals were on the video for the whole time.

Three minutes after the beginning of the recording, a playback of 10s was played with a portable speaker (MegaVox Pro MEGA—7500, Anchor®) and recording went on for 3 minutes. The playback was either the call of a common bird (control) or the roar of a lion (treatment) simulating a context of immediate predation. Two bird species were chosen as control, because of their relative commonness in the area: the Grey Lourie (*Corythaixoides concolor*) and the Red-eyed Dove (*Streptopelia semitorquata*).

The experiment was conducted on 21 harems, with a total of 76 individually identified adult zebras. We did not analyse the behaviour of young zebras, as they may have a poor perception of predation risk and show non-adaptative behaviour, making it difficult to interpret their vigilance levels (Arenz and Leger 2000). Every group was tested with a lion call, with one or two replicates, for a total of 32 observation sequences. In addition, 12 of those harems were tested with the control playback.

Additional information was collected on the site of the experiment: distance to the closest cover was estimated after filming, using a range finder from the group position at the moment of the playback. Grass biomass was estimated using a disk pasture meter on 6 randomly chosen points at the place where the group was feeding during the experiment. We also recorded the strength of the wind, which could have an influence on the behaviour of the individuals. As perception of predation risk might change with the distance to the stimulus, we noted the distance of the harem to the speaker used to play the sound. Social information was also noted, like group size and composition, and reproductive status of individuals (presence of a foal with the mother).

Using the video footage, we then coded for every individual its behaviour during the whole recording (noting the type of behaviour and its duration). No ambiguity was encountered in the determination of behaviours.

Data analysis

Test for the experimental validity of the treatment

We tested the reliability of the playback experiment by comparing the response to the lion playback and to the control playback. We thus computed a generalized linear mixed model using glmer function of lme4 package with R-software, version 2.15.1 (R Development Core Team 2012), on the length of the first vigilance bout after the playback using Poisson distributed errors with the same random structure as in models thereafter, with calling type (lion or control) as an independent variable. We also controlled for all the variables included in other models. We estimated the effect size of the playback type and its confidence interval with parametric bootstrapping (10000 replications, see explanations below).

Analysis of the importance of fixed effects

We analyzed which factors influenced vigilance levels before and after the lion roar playback.

Before playback

Individuals can adjust their vigilance in several ways: by changing the frequency, or the time they spend being vigilant. The frequency of vigilance, the fraction of time spent vigilant and the mean length of vigilance bouts were highly correlated (the correlation coefficient was 0.66 for frequency and fraction; 0.28 for frequency and mean; 0.84 for fraction and mean), so we ran the analysis only on the frequency of vigilance.

For this analysis, we built a generalized linear mixed model using Poisson distributed errors, with a random intercept on the individual nested in the group it belonged to.

The model included as fixed effects the distance to cover, group size, grass biomass, wind strength and reproductive status (Male vs. Female vs. Female with a foal). We also controlled for the distance to the speaker and for the number of the experiment on the group (first vs. second lion roar playback), to see if there was a habituation of individuals to the experimental design. All continuous variables were centered.

Effect sizes of the fixed effects and their 95% confidence intervals were calculated with parametric bootstrap (10000 replications) on the output of the model. Parametric bootstrapping consists in fitting a linear mixed-model on real data, extracting random values from the distributions of estimates parameters (grand mean, variance of random effect, residuals variance), generating from these values a new dataset with the same correlation structure, sample size and distribution of measurements across groups, and fitting on this simulated dataset a new linear mixed-model.

There is no consensus on what kind of R² statistics to use in linear mixed models. As we were interested in the importance of fixed effects in terms of improvement of the fit, we chose to use the formula proposed by Edwards et al. (2008), which compares the full model to a null model with all fixed effects deleted (except the intercept), with the same random effect structure. This R² statistic thus gives an idea of the importance of fixed effect in explaining observed variations of the analyzed variable.

After playback

To look at the factors influencing the way individuals adjust their vigilance in a situation of high predation risk, we chose to work on the length of the first vigilance bout after the playback. We assumed that the riskier the situation was perceived, the longer the vigilance bout lasted.

For this analysis, we also built a generalized linear mixed model using Poisson distributed errors with the same random effect structure. This model included the same independent variables tested before. Effect sizes of the fixed effects and their confidence intervals, and the importance of these effects in terms of quality of fit were estimated with the same methods.

Repeatability of behaviour in groups and individuals

For this analysis we only included the sequences for groups and individuals that had been exposed to the lion roar playback twice. The aim of this test was to look at the differences in repeatability of behaviour between groups and individuals when risk of predation is low or high.

To evaluate the individual and group constancy across measurements, we computed repeatability, measured here using the Intraclass Correlation Coefficient (ICC, Nakagawa & Schielzeth 2010). It is a measure widely used in a broad range of fields such as social sciences, evolutionary biology, community ecology (Siddiqui et al. 1996; English et al. 2010; Violle et al. 2012) and behavioural ecology (van Oers et al. 2004; see Bell et al. 2009 for a review). In the context of glmm an ICC measures the proportion of variance – which remains after accounting for the fixed effects – accounted for by a random effect. Here we calculated between-individual ICC with individual ID nested in groups, which measures the constancy of intra-group individual differences. We also calculated between-group ICC, which measures the constancy of between-group differences in mean vigilance levels. Finally, the constancy of between-individual differences, across all individuals (irrespective of their group) was also calculated.

Note that given its calculation ICC actually measures the relative repeatability, i.e. the consistence of between-individual or between-group differences, not repeatability of the absolute level of the behaviour.

We used the variance estimates of random components (resp. Individual nested in Group, Group, Residuals) from the generalized linear-mixed models presented above, without fixed effects, and keeping the same random structure, still separating before and after the playback, to compute both group and individual repeatabilities. The exact formulas used for glmer with Poisson distributed errors are reported in Nakagawa & Schielzeth (2010) .

95% confidence intervals were calculated for all ICCs with parametric bootstraps (10000 replications for each bootstrap) on the output of the different models.

RESULTS

Experimental validity of the treatment

The length of the first vigilant bout after the playback was significantly longer when playing the lion roar than when playing the sound of a control bird (effect size = 0.442, 95% CI: 0.100 – 0.785).

Before playback

Before the playback, few fixed effects had a significant effect on the frequency of vigilance (Fig. 1). Females without foals were significantly less vigilant than males (effect size = -0.286; 95% CI: -0.556 – -0.010, taking males as reference), but were not different from females with foals. Zebras tended to be less vigilant in bigger groups (effect size = -0.059; 95% CI: -0.162 – 0.043) and when far from the cover (50-100 m away, effect size = -0.061; 95% CI: -0.566 – 0.437; > 100m away, effect size = -0.286; 95% CI: -0.706 – 0.136, when taking 0-50m as reference).

The percentage of the variance explained by the fixed effects was small, as the calculated R^2 value was equal to 0.13.

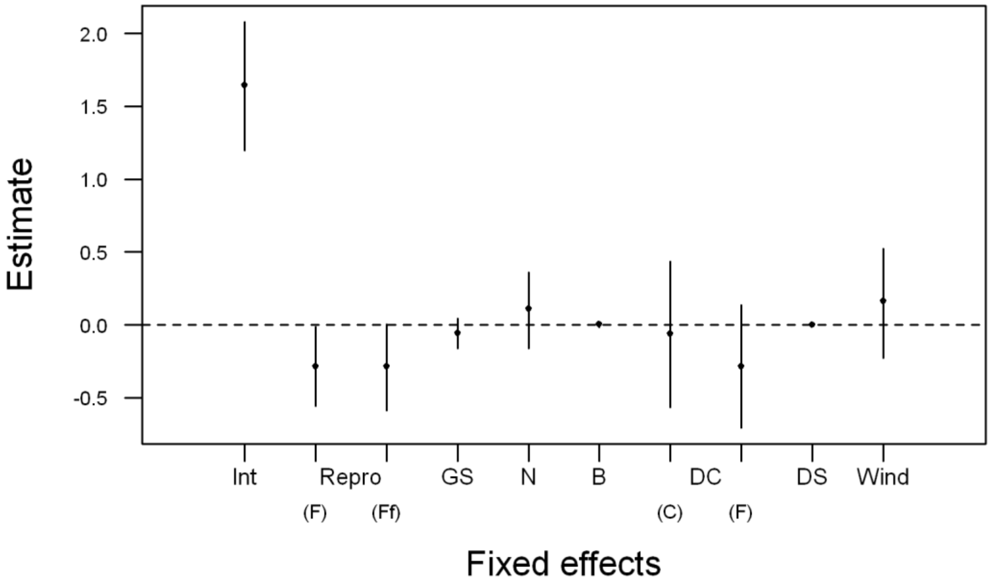

Figure 1. Effect size and 95% confidence intervals computed by parametric bootstrap (n=10000 replications) for coefficient estimates of fixed effects from the generalized random model explaining variations in frequency of vigilance before the playback. Int: Intercept; Repro: Reproductive Status (F: Female, Ff: Female with foal; male was taken as reference); GS: Group Size; N: n° of experiment; B: Grass Biomass; DC: Distance to Cover (C: 50-100m; F: > 100m; 0-50 m was taken as reference); DS: Distance to Speaker.

After playback

After the playback, the first vigilant bout was significantly shorter for females (effect size = -0.425; 95% CI: -0.806 – -0.034, Fig. 2) and females with foals (effect size = -0.447; 95% CI: -0.869 – -0.028, Fig. 2) than for males. When far from the cover zebras were also less vigilant after the playback (50-100m effect size: -1.253; 95% CI: -1.995 – -0.557; > 100m effect size: -0.834; 95% CI: -1.463 – -0.211, Fig. 2). When there was wind, zebras stayed longer in the vigilance posture (effect size = 0.761; 95% CI: 0.186 – 1.321, Fig. 2) just after playing the lion roar. When far from the speaker, zebras were also less vigilant, but with a small effect size (effect size = -0.015; 95% CI: -0.030 – -0.0008, Fig. 2). In larger groups, zebras still tended to be less vigilant (effect size = -0.149; 95% CI: -0.308 – 0.015, Fig. 2). The other fixed effects were not significantly different from 0 (Fig. 2).

The R² value of fixed effects after the playback was higher than before the playback (R² = 0.30).

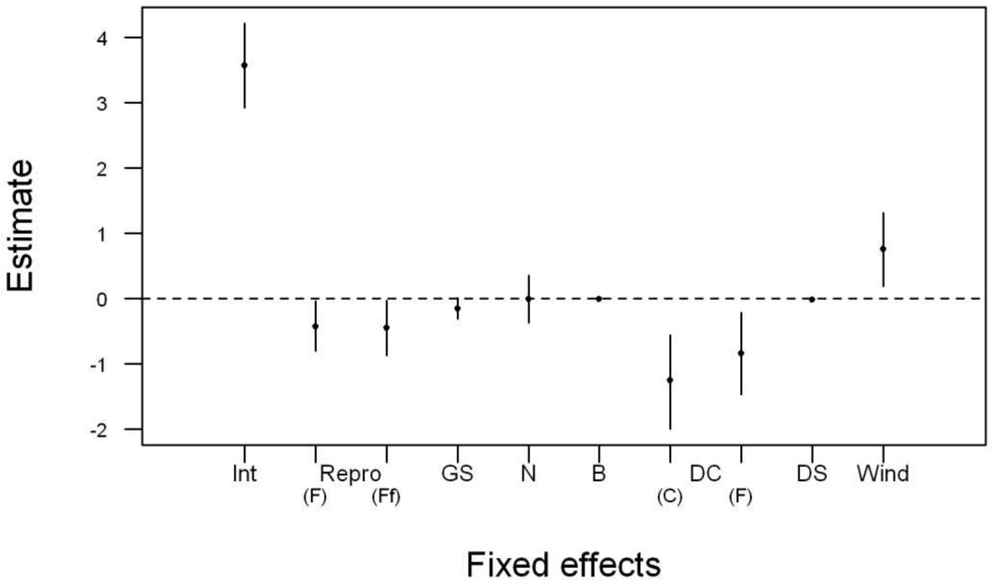

Figure 2. Effect size and 95% confidence intervals computed by parametric bootstrap (n=10000 replications) for coefficient estimates of fixed effects from the generalized random model explaining variations in the length of the first vigilance bouts after the playback. Int: Intercept; Repro: Reproductive Status (F: Female, Ff: Female with foal; Male was taken as reference); GS: Group Size; N: n° of experiment; B: Grass Biomass; DC: Distance to Cover (C: 50-100m; F: > 100m; 0-50 m was taken as reference); DS: Distance to Speaker.

Repeatability of vigilance behaviour

Repetabilities of vigilance behaviour were very low: before the playback, estimates were less than 0.05 and were not significantly different from 0 (Fig. 3). However, the 95% CI were really large.

After the playback, repeatability of the behaviour of individuals nested in groups was null, but the estimate of repeatability of the group was higher than before the playback (repeatability = 0.12). However, the 95% confidence interval still included 0 (Fig. 3). As expected then, the estimate of individual repeatability in the population was equal to the estimate of the group repeatability.

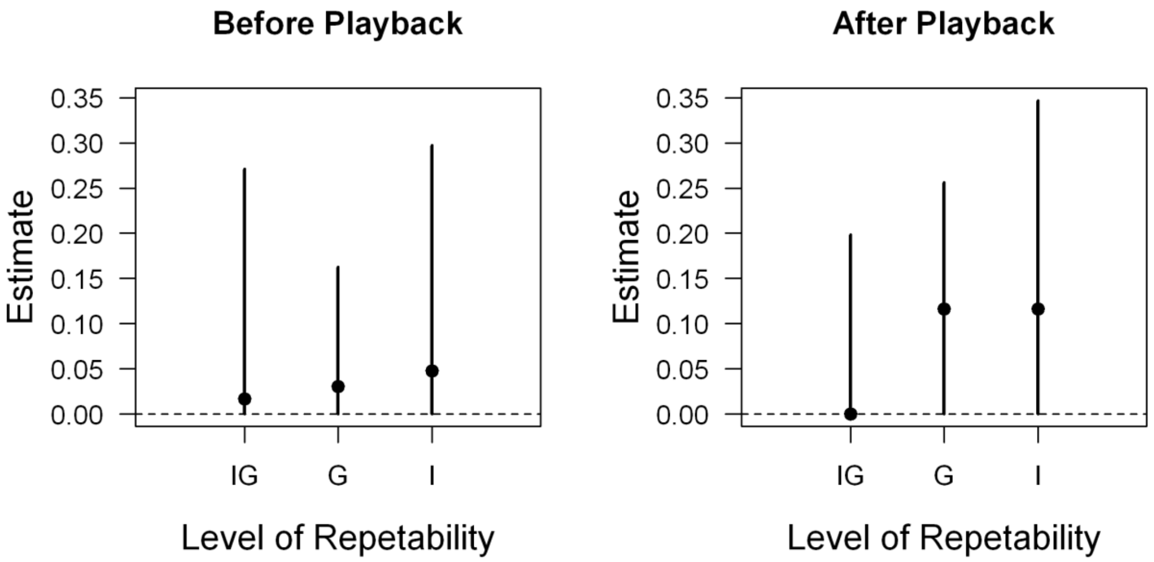

Figure 3. 95% confidence intervals of repeatabilities computed by parametric bootstrap (n=10000 replications) from variance estimates of random components of the model explaining variations in frequency of vigilance before the playback and in the length of the first vigilance bouts after the playback. IG: Individual nested in Group; G: group; I: Individual.

DISCUSSION

Before the playback, the environmental and social factors did not explain much of the variation in vigilance behaviour, as the variance explained by the fixed factors was 13%. The results were however consistent with the literature. Zebra males were more vigilant than females as found by Burger and Gochfeld (1994). This is consistent with the mating biology of zebras: the harem males are alert for attempts by bachelors to approach their females (Ginsberg & Rubenstein 1990). Surprisingly, we found that females with foals were not more vigilant than females without young. This result differs from Childress and Lung (2003) who showed that female elk with calves are preferentially targeted by wolves *Canis lupis* and are consequently the most vigilant age/sex class. As females with foals are lactating, they have high nutritional needs, and may thus spend more time feeding and less time vigilant. The total number of individuals in the group, i.e. “group size effect” tended to decrease vigilance in zebras, as widely discussed in the literature (Roberts 1996). This effect might be non-significant because of the small variation in size of zebra harems (between 2 and 5 adults). Grouping of different zebra harems can occur in the wild, but in this experiment we specifically avoided large groupings of harems, as we wanted to analyse behaviour at the harem level. The lack of significance of the factors we tested might be due to the short length (3 minutes before the playback) of the behavioural sequences; adjustments in behaviour might have occurred at a longer time-scale. It is however hard technically to film entire groups for a longer time. Although longer monitoring may have allowed detection of more subtle effects, our results suggest that none of the effects studied here strongly affected vigilance levels in routine conditions, i.e. when no immediate predation risk was perceived.

After the playback, more environmental and social factors influenced the vigilance behaviour of zebras, and they explained more of the variation in vigilance behaviour. Zebra males were still more vigilant than females, and females with foals were still not more vigilant than females without foals. This is still consistent with our hypothesis of the impact of the high energetic demands of lactation. Vigilance also increased when zebras were close to the cover. Lions are ambush predators (Schaller 1972), and cover might thus be perceived as dangerous by zebras, especially when hearing cues implying the presence of a predator. In the literature, the effect of distance to cover has been widely discussed, and is quite variable, mainly depending on whether prey perceive the cover as obstructive or protective (Lima 1990). This result strongly suggests that cover is perceived as obstructive by zebras. When there was wind during the experiment, the first vigilance bout after the playback was lengthened. The presence of wind may induce stress, by either removing important clues of predation like odours or sounds, preventing the individual to correctly evaluate the predator’s position after the roar has been heard, or by creating false indications of the predator’s position by moving the grass. The effect of distance to speaker, although small, was significant, meaning that zebras were less vigilant when the speaker was far. It shows that zebras can evaluate the distance at which the roar is played and judge the riskiness of the situation. The percentage of variance explained by the fixed effects was much higher after the playback (30%) than before. When facing direct predation, zebras thus seem to rely more on environmental and social cues to interpret how risky the situation is. When they are facing a direct threat and are in a risky situation, for example close to the cover, or close to the threat (here, the speaker), zebras adjust their levels of vigilance in consequence. This is consistent with the findings from Periquet et al. (2012) who found that presence of lions in a radius of 2 km from zebras changed their vigilance behaviour.

Repeatabilities of vigilance behaviour were very low before playback and non-significantly different from 0. After the playback, repeatability of the behaviour in groups tended to be higher (around 12%), but still not significantly different from 0, and repeatability of behaviour of individuals in the population was due to the group they belonged too. It seems again that direct hazard may influence the behaviour of zebras, with some groups more vigilant than others. Groups may have consistent differences in their antipredation strategies: some groups investing more in temporal or spatial avoidance, other being more vigilant. It also seems that groups might be different between them while not having much variance within them, as the repeatability of the behaviour of individuals was due to the group repeatability. The group may indeed be the unit of control of individual behaviour (Conradt & Roper 2003). We must however be cautious with our conclusions, as all 95% confidence intervals of repeatability estimates included 0.

There seemed to be no consistency of the vigilance behaviour of the individuals. This might mean that vigilance behaviour in zebras is not a personality trait, perhaps due to the high pressure of predation by lions, counter-selecting too much variability in this trait. Or other constraints, like constraints on foraging time, due to the poor quality of the diet available, might reduce variations in vigilance. However, we still need to be cautious, as the confidence intervals of repeatability estimates were very large. This might be due to high variations in vigilance behaviour, making only 2 repetitions inadequate to capture the repeatability of this behaviour, contrary to what was observed in many other study of animal personality, in which two repetitions were enough to find consistency in some behaviours (as reported in the review of Bell et al. 2009).

This study, consisting of a series of playback experiments in the wild, confirmed that we need to be cautious with our conclusions when studying vigilance, because it is a very variable behaviour. Indeed, environmental and social factors explained very little of the variance in this behaviour in routine conditions. However, we were able to show that the use of these environmental and social cues by zebras differed when they were facing a hazardous situation: when in the presence of lions, zebras are more sensitive to their surroundings and the riskiness of their spatial position. There was no consistency in the behaviour of individuals or groups, even if there was a tendency for groups to act more consistently when in risk of direct predation, showing that the group could play an important role in shaping characteristics of individuals. Direct risk of predation induced by a playback of a roar strongly influences the behaviour of animals and changes their perception of the world around them. It is thus important not only to study vigilance behaviour in normal contexts, but also in risky contexts, which may change the effects of environmental and social factors. These changes of behaviour when the predator is detected are important both for the predator and the prey. As stated by Lima (2002), it is important to put the predator back in predator-prey interactions: predator chances of killing a prey are probably greater when remaining undetected; they should thus choose to prey on unaware individuals or groups. This also underlines the importance of detecting predators for zebras, as they might be more vulnerable when they are not aware of them, having not assessed the real riskiness of their position.

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Chapitre V

Diet quality in a wild grazer declines under the threat of predation

Diet quality in a wild grazer declines under the threat of predation

In preparation

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INTRODUCTION

Whereas the link between the consumptive – lethal - effects of predation and population dynamics (through survival) is straightforward, the link between the non consumptive effects of predation and population dynamics is less obvious and has been so far understudied. However, the non consumptive effects of predation may carry significant costs through their influence on the energetic and physiology of prey (Creel et al. 2007; Creel & Christianson 2008; Creel et al. 2009). As emphasized by a meta-analysis principally involving invertebrates, predators can even have a greater effect on their prey's demography through behaviourally mediated effects than through direct consumption (Preisser et al. 2005; see also Schmitz et al. 1997). Hence, there is a real need to identify and quantify the costs associated with the prey behavioural shifts resulting from predator avoidance to fill the gap between behaviour and fitness. In particular, nutritionally mediated risk effects are of high interest, as the quantity/quality of resources ingested is likely to influence prey maintenance, survival and also reproduction.

Large mammalian herbivores (herbivores hereafter) face a trade-off between foraging and predation avoidance (Olff et al. 1999; Fortin et al. 2004) and have been shown to use a wide array of behavioural adjustments to the presence of their predator, in particular habitat shifts (sometimes towards sub-optimal habitats regarding foraging) (Creel et al. 2005) and increase in vigilance level (Laundre et al. 2001). Hence, the presence of predators is likely to have a detrimental nutritional effect, as shown for at least one population of large herbivores in the wild (Christianson & Creel 2010). More studies in the wild are however needed to understand better how predators affect the diet of their prey, generalize these findings, and unravel the underlying mechanisms (habitat shift vs. vigilance increase).

In semi-arid regions, especially in low-nutrients soil savannas of the southern hemisphere, plants offer low quality of proteins because of the poor quality of the soil. Plant quality is also generally characterized by complex spatial heterogeneity (Frank 2006). Additionally, crude protein content of the diet is highly important for non-ruminant herbivores as some essential amino-acids cannot be synthesized by the animal and can only be acquired in their diet (Sinclair et al. 2006). Herbivores, and particularly non-ruminant herbivores, are therefore particularly constrained in these regions, and anything influencing the selection of plants of good quality could have a detrimental impact on the fitness of individuals.

In Hwange National Park, Zimbabwe, Plains zebras (*Equus quagga*) experience high feeding constraints due to the poor quality of available forage and are one of the main prey of lions

(*Panthera leo*, Loveridge et al. 2007). Predation by lions has been suggested to have strong effects on zebra population dynamics in this ecosystem (see Chapter II). Additionally, behavioural studies have shown that, when chances of encountering lions are high, zebras tend to change their habitat selection (Fischhoff et al. 2007; Valeix et al. 2009), and increase their vigilance level (Periquet et al. 2012). Hence, we used combined data from GPS-collared zebras and lions and collection of individual zebra faeces to test the hypothesis that the diet quality of zebras decreases when lions have been in their vicinity. Such relationship could arise from two possible underlying mechanisms: either because zebras shifted their habitat for safer habitats that might be of lesser quality, or because zebras spent more time vigilant when predators were around, leaving less time to select plants of higher quality.

MATERIAL AND METHODS

Study area

The study was carried out in Hwange National Park in western Zimbabwe (19°00'S, 26°30'E). The park covers ca. 15,000 km² of semi-arid savanna. The mean annual rainfall is 606 mm and there are two main seasons: a dry (May-October) and a wet (November-April) season. The vegetation is dominated by deciduous woodlands and shrublands, with patches of grasslands (Rogers 1993).

Plains zebras are a gregarious species and form non-territorial harems consisting of a stallion, one or more female(s) (generally not more than five) and their foals (Klingel 1969). Individuals of a harem move together and are seldom separated.

The study population of Plains zebra moves freely within the Main Camp area (approximately 1,000 km²) in the northern part of the Park and has been monitored since July 2004. Because of their unique stripe patterns, zebras can be identified individually. A database of known individuals was therefore available, with information on individuals gathered every 6 months. During monitoring periods all encounters with harems are recorded, with the precise time of encounter and location, as well as the group composition.

Zebra and lion GPS data

Seven zebra harems were closely monitored for the purpose of this study. We equipped one female with a GPS radio-collar in each harem. GPS locations were taken on an hourly basis 24 hours a day.

As part of the long-term monitoring of the lion population in Hwange National Park, several lions have been equipped with GPS radio-collars over the past ten years. We used data from 10 GPS radio-collared lions (7 males and 3 females) that were in the study area for the 7 zebra harems at the time of this study (Fig. 1). For each lion, one location was available hourly from 6 pm to 7 am.

Faecal sample collection

In order to determine the quality of the zebra diet we collected dung samples from known individuals from the database: 164 samples from 49 individuals in 17 harems were collected from individuals which were observed defecating during the wet and the dry season of 2010 (between February and March and between August and October), particularly focusing on the GPS-collared equipped groups. For each dung, we collected a sub-sample representative of the dung pile, and dried it within 48 hours, either air-drying or in a low heat (40° C) field oven. The samples were packed in plastic bags and stored dry at room temperature until assayed.

Mean retention time in equids is around 44.5 hours (Duncan et al. 1990). Dung samples thus represent an integrative measure of the quality of the diet of the previous 1 to 3 days. Events happening before those 44.5 hours can have a direct effect on the quality of the sample.

Analysis of diet quality

Chemistry analyses were performed in the chemistry lab of INRA-URP3F (Lusignan). All samples (164) were ground (1 mm grid) and analyzed by Near-Infrared Spectroscopy (NIRS). On 100 randomly chosen samples, Nitrogen content was determined by the Dumas method (Dumas 1831) on a Flash 2000 Organic Elemental Analyzer. 80 samples out of the 100 were used to build an equation of prediction of N content by NIRS. This equation was tested with the 20 remaining samples to check the quality of the prediction. Eventually, an equation was built based on the 100 samples. The coefficient of correlation between prediction and manual measurements was 0.92, with an R² of 0.85. This equation was used to predict N content for all the 164 samples. Crude Protein (CP) content was calculated by multiplying the N content by 6.25. All values of CP used for statistical analyses correspond to predicted values from NIRS

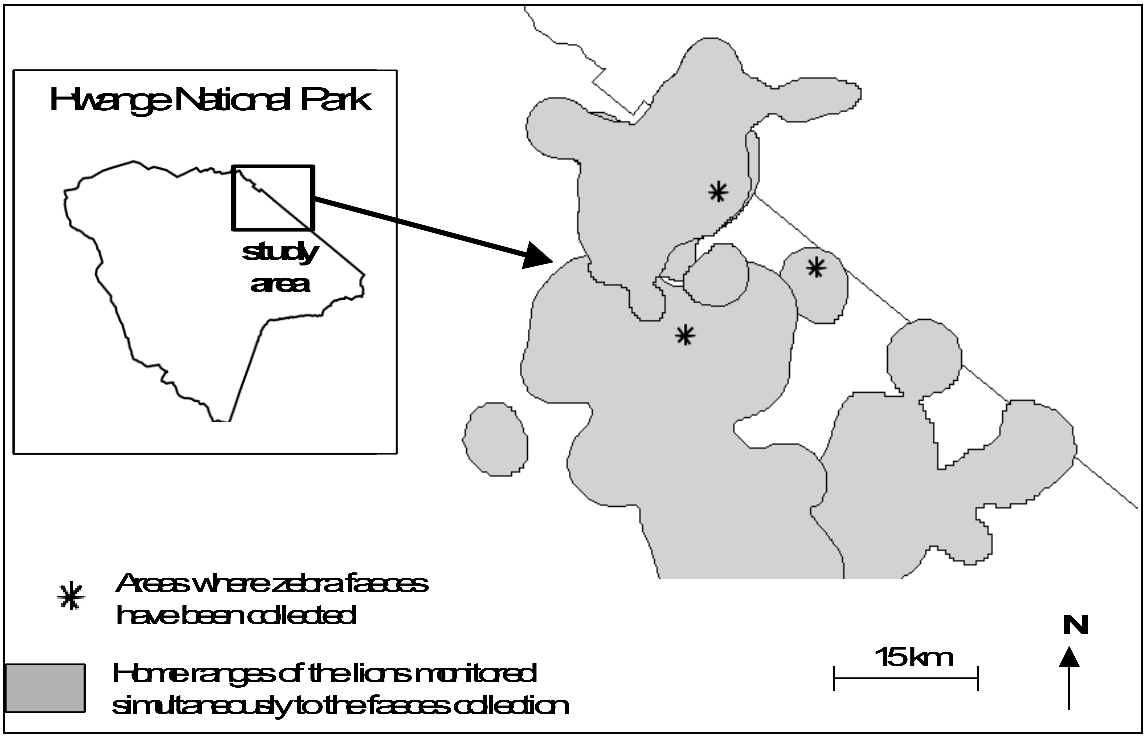

Figure 1. Map of the sampling locations of faeces and home ranges of lions monitored during sampling sessions (Wet season 2010).

Index of predation risk

As lions are mainly active during the night, risk of predation is higher for prey during these periods of higher activity (Schaller 1972). Furthermore, lion data were available continuously only during nights. We therefore calculated an index of predation risk only during the night (from 6 pm to 7 am).

As mean retention time in equids is around 44.5 hours (Duncan et al. 1990), we used GPS data from the night at least 44.5 hours before sampling and the night before that one (Night -2 and Night -3 before sampling), assuming that encountering lions could have either a short term effect or an effect on a longer term. For each night we calculated the distance between zebras and lions every hour between 6 pm and 7 am. We kept the minimum distance between zebras and lions during those two nights as an index of predation risk.

When there was no GPS data available for the zebra harem, we used known information on locations of zebras during the days before sampling. Observations were mainly made during early morning (5.30 to 11 am) and late afternoon (4 to 6.30 pm). We only used observations made during early morning, as zebras seldom move at night (Estes 1991). We thus calculated the distance between the location of the observation and lion positions between 6 pm the previous evening and 7 am the same morning (for Night -2 and Night -3 only). We also kept the minimal distance to a group of lion as an index of predation risk.

If there was no information on the position of zebras, either with GPS collars or with the monitoring data, the sample was removed of the analysis of the effect of distance to lions.

Data analysis

As there were only few samples during the dry season with known locations for zebras, we only used samples from the wet season. In total 60 samples from 32 individuals were used in the analyses.

We used linear mixed models with random slopes (function lmer of package lme4 using R software, R Development Core Team 2010) with CP content of the faeces as a dependant variable. We included a random intercept associated with the interaction of the date of sampling and group identity, taking account of the fact that samples coming from members of a same harem on a same date were correlated. We also included a random intercept on individuals nested in their groups, to take account of repeated measures on individuals and groups. A random slope on the effect of distance to lions between individuals nested in groups was also included, to allow for different reactions to risk of predation between individuals and in-between groups, and also to have better estimates of the effects and reduce type I error (see Schielzeth & Forstmeier 2009 for a better hindsight on why to use random slope models instead of random intercept model).

The fixed effect tested was the effect of distance to lions, using classes of distance: lions closer than 2 km (Close) and lions further than 2 km (Far). There are no certainties about the distance at which zebras can detect presence of lions but several studies have shown that zebras could adjust their behaviour to the presence of lions within a 2 km radius (Valeix et al. 2009; Periquet et al. 2012). All known prides in the area included at least one collared lion and lions from the same group tend to stay together most of the time. In addition, lions are territorial, and home ranges of the monitored lions clearly encompassed the monitored area (Fig. 1).

We also controlled for the sex of the individual in the model, as males and females might differ in the quality of the diet they are ingesting (for example in Camargue horses, male diet quality if worse than females', Duncan 1992)

A likelihood ratio test was conducted between the model with the distance to lions and the model without any effect of distance to lions (in the fixed and random structure). As there are some controversies on the use of LRT in mixed models, we also computed ninety-five percent confidence intervals on effect size using parametric boostrap (10000 replications). Because the results of the LRT were consistent with the parametric bootstrap, we will only present the results of the latter.

RESULTS

There was no effect of sex on the CP content of the faeces, but males tended to have lower CP content than females (Fig. 2).

CP content in the faeces of zebra was lower when lions had been close around foraging time than when lions were further away. As the lower limit of the 95% CI interval only slightly encompasses 0 (effect size = -0.65; 95% CI: -1.307 – 0.0608) and the 90% CI is -1.1853 – -0.0552 (more than 95% of the estimates are thus under 0; Fig. 2), we feel confident about the significance of this effect.

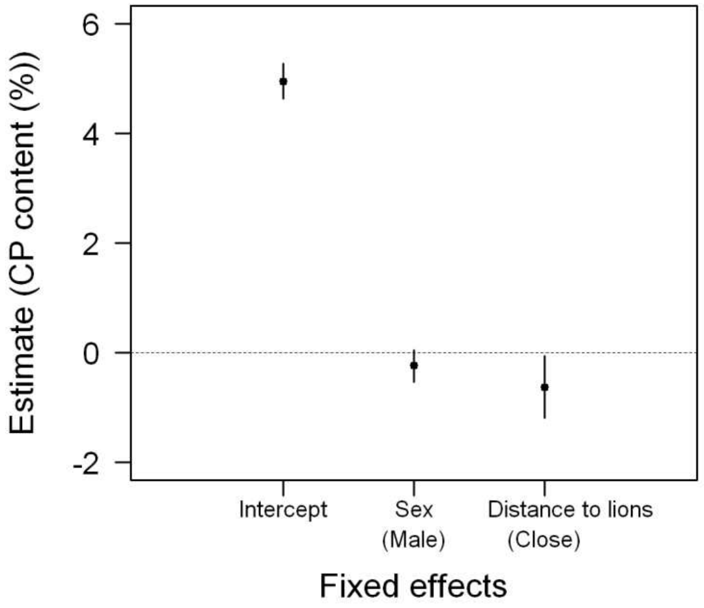

Figure 2. Effect size and 90% confidence interval computed by parametric bootstrap (n=10000 replications) for coefficient estimates of fixed effects from the full random slope model explaining variations in CP content.

DISCUSSION

Our results show that the crude protein content of zebra faeces was lower when they had been in the vicinity of lions sometimes within the past 3 nights. To the best of our knowledge only Christianson and Creel (2010) have previously showed a detrimental effect of predator presence on diet quality in a wild large herbivore. The fact that zebra diet quality is lower when lions have been in the vicinity means that the adjustments in behaviour when lions are within short distance (see Fischoff et al. 2007; Valeix et al. 2009; Periquet et al. 2012) have nutritional costs. The decrease in diet quality detected here could arise from two types of behavioural adjustments: zebras could have shifted their habitat for safer habitats that might be of lesser quality, or zebras could have spent more time vigilant because of the vicinity of predator, leaving less time to forage selectivity towards bites of higher quality.

To gain insights into the likely underlying mechanism, we compared characteristics of zebra movements when lions were absent and when lions were present. We used the GPS data available for the zebras for which we had samples used in the previous analyses. For each sample where zebras had been close to lions (either during the Night -2 or Night -3) , we calculated for 24 hours, starting from the 1st point where lions were closer than 2 km (during the night), the path length, the net displacement, the average speed, the mean turning angle and the straightness index of the trajectory. The straightness index is the net displacement divided by the total path length; it ranges between 0 (very convoluted path) and 1 (straight line). We compared these trajectories with randomly chosen 24 hours trajectories for zebras which had been further than 2 km to lions, starting at a random point during the night (between 6 pm and 7 am), randomly choosing the night (Night -2 or Night -3 before the sample) as well. When lions were close, the zebras showed short net displacements (mean net displacement around 500 m) and tortuous trajectories (see Fig. 3), so they moved less and did not leave their area. The zebras thus did not change habitat by moving far from lions. This gives weight to the hypothesis that zebras mainly adjust their vigilance when lions are close as found by Periquet et al (2012), maybe moving less to reduce chances of encountering them, but we cannot exclude the fact that they might have adjusted their habitat use by making micro-changes that are not detectable at the GPS-level. These are however preliminary results, because only 22 full 24-hours trajectories were available for this study. Studies on more trajectories are thus needed to confirm these results. While habitat shifts due to predation pressure have been documented (e.g. Fortin et al. 2005), changes in movement characteristics of prey have been less studied. In a study on plains zebras, Fischoff et al. (2007) found that zebras increased their speed and took sharper turns in grasslands during the night, when risk was high. There was, however, no information on direct lion presence. More precise studies on how prey move when facing direct risk of predation are thus needed.

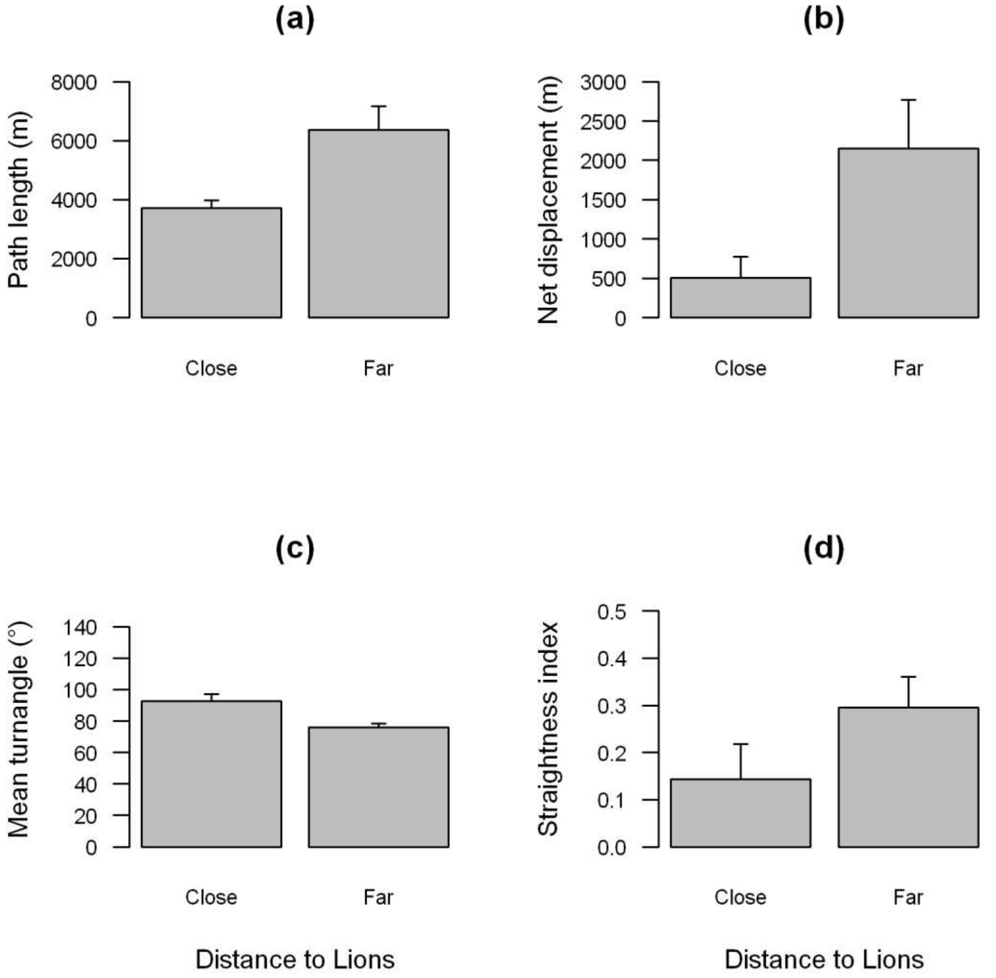

Figure 3. Effects of distance to lions (close vs. far) on different characteristics of 24 hours trajectories of plains zebras: (a) path length, (b) net displacement, (c) mean turning angle and (d) straightness index. Error bars are standard errors.

This study also provides insights into the likely cost associated with the anti-predator behavioural adjustments made by zebras when lions are in the vicinity. Even if the effect of distance to lions on the CP content of the diet seems to be small (less than 1% difference in CP content), the models only test the mean effect on the population, and there are high differences between extreme points in these two contrasted situations; close to lions quality can be as low as 4% CP, whereas far from lions it can be as high as 8% (Fig 3). This difference could be really costly to individuals, as they need to compensate for low quality by eating more forage. Indeed, if we assume that the mean protein requirement for zebras is 392 g/24 hours (calculated from horses of same weight, Abaturov et al. 1995) and that CP digestibility is around 35% (Abaturov et al. 1995), zebras being close to lions would need to forage 18 kg of grass, whereas zebras far from them would only need to eat 9 kg of grass. For a same intake rate, zebras under threat of predation would thus need to spend almost twice as much time for foraging to compensate for the poor quality of their diet.

Figure 4. Effect of distance to lions (close vs. far, the threshold being 2 km) on the Crude Protein content of plains zebras faeces.

Diet quality of the zebras in HNP is particularly low as mean CP content for our samples during the wet season was only around 5.3 %. Other studies on plains zebras have reported higher values (Abarutov et al. (1995): 6%; Edwards (1991): 7%; Codron et al. (2007): 7.5 %). Combined with this low quality of forage, the predation risk is high, as the ratio predator/zebras is high compared to other areas (see Chapter II): our zebra study population is thus highly impacted by the presence of lions probably because of the poor quality of forage available. Zebras need to select forage of high quality, but when threat of predation is high, they cannot be very selective. This induces a deficiency in nutrients which would then need to be compensated by spending more time to eat, leaving less time to avoid and detect predators, conducting zebras to be more vulnerable to lions. This could partly explain the observed decline in the zebra population since the end of the hunting quotas on lions and the subsequent increase of lion population (see Chapter II).

This study thus highlights that behavioural responses to predation risk can be costly in terms of nutrition for the prey. This is consistent with previous findings from Christianson and Creel (2010), who found changes in diet of elks due to wolf presence. They hypothesized that these changes might have been sufficient to reduce survival and reproduction in their population. In our study population, zebras seem to be always in good body condition (P. Duncan, F. Barnier, pers. obs), thus the poor quality of their diet might not affect directly their survival. However, it might induce the need to forage for longer times, and thus prevent zebras to mount strong antipredator responses, leading to higher predation rates. This also confirms the need to investigate the costs associated with the indirect effects of predation when studying prey populations, as effects on the nutrition of prey by the mere presence of predators could easily be mistaken for other effects, like bottom-up effects (as pointed by Christianson & Creel 2010). More studies are still needed to better understand the proximal causes of these changes.

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Discussion

Discussion

1. Synthèse

Durant cette thèse, mon travail a été centré sur l’étude d’une espèce de grand herbivore, le zèbre des plaines. En utilisant des approches à la fois au niveau de la population et au niveau individuel, et en combinant la dynamique des populations et l’écologie comportementale, j’ai essayé de déterminer quel impact la prédation pouvait avoir sur cette espèce dans un environnement particulier : le parc national de Hwange, au Zimbabwe.

La première section de la thèse visait spécifiquement à mieux comprendre la dynamique de populations de zèbres dans le parc de Hwange. La première partie du premier chapitre, qui est méthodologique, a contribué à mettre en évidence les techniques de détermination de la grossesse chez le zèbre des plaines. Comme les zèbres femelles peuvent donner naissance pendant toute l’année et que nous les suivons uniquement tous les six mois, il est en effet difficile de déterminer les taux de fécondité des populations de zèbres. En outre, de nombreuses naissances peuvent ne peut pas être détectées parce que certains jeunes ne survivent que quelques jours et donc ne sont jamais vus sur le terrain. Le suivi hormonal permet de se débarrasser de ces contraintes, car il suffit d’échantillonner régulièrement les femelles, par exemple tous les six mois, afin de détecter une grossesse. Cette méthode non-invasive est donc un outil utile pour surveiller la reproduction chez les populations sauvages (Linklater et al., 2000). Elle pourrait également être couplée avec des informations sur les individus pour déterminer le succès reproducteur des femelles au niveau individuel. Dans la seconde partie de ce chapitre, je me suis intéressé aux facteurs qui influencent le temps entre deux naissances consécutives chez une femelle zèbre. Bien que cet élément ne soit pas central dans la compréhension des effets de la prédation sur la population de zèbres, il permet d’avoir une meilleure idée des caractéristiques de la dynamique de la population dans notre zone d’étude et des coûts potentiels de la reproduction. En effet, il semble plus coûteux pour une mère d’avoir un poulain mâle que femelle, car il faut plus de temps pour les femelles pour avoir un autre poulain après avoir donné naissance à un mâle. Ce coût pourrait affecter les activités anti-prédatrices, les femelles ayant moins d’énergie à investir dans celles-ci et étant ainsi plus vulnérables à la prédation. En utilisant les informations obtenues à partir des échantillons fécaux et à partir du suivi individuel des femelles, nous avons pu déterminer le taux de fécondité de la sous-population suivie, qui est très proche des taux obtenues lors d’autres études sur les zèbres des plaines dans d’autres écosystèmes (comme dans le parc du Kruger, Smuts, 1976).

Dans le deuxième chapitre, nous avons utilisé des méthodes de capture-marquage-recapture pour calculer les taux de survie pour différentes classes d’âge de zèbres et pour examiner les différences de survie entre sexes. Cela nous a permis de construire un modèle de dynamique de population, en utilisant le taux de reproduction des zèbres déterminé dans le chapitre I. Ce modèle confirme le déclin de la population de zèbres suivie, un résultat cohérent avec les données de comptage par transect routier qui sont menés chaque année. Ceci démontre que les estimations de survie et de fécondité de la population étudiée ne sont pas loin de la réalité. L’augmentation de la densité des lions en parallèle avec le déclin de la population de zèbres suggère que les deux pourraient être liés. En comparant la dynamique de populations des zèbres du Serengeti à ceux de Hwange, nous avons pu montrer que le déclin observé est principalement dû à la faible survie des jeunes classes d’âge. Ce faible taux de survie est probablement lié au coût de la dispersion dû à la prédation, avec une prédation plus importante sur les individus qui dispersent (les zèbres sont plus sujets à la prédation par les lions quand ils sont seuls que lorsqu’ils sont en groupes, Schaller, 1972). En raison de leur longue période de gestation (12-13 mois) et parce que seulement un poulain naît à chaque gestation, les zèbres ne peuvent pas compenser ce faible taux de survie, ce qui pourrait être la raison de la baisse observée de la population sous une forte pression de prédation.

La deuxième partie de la thèse s’est intéressée à la compréhension plus détaillée des réponses anti-prédatrices mises en œuvre par les zèbres au niveau individuel, notamment en termes de changements de comportement. Dans le troisième chapitre, nous avons étudié le compromis entre le comportement de recherche de nourriture et celui de vigilance, en nous intéressant particulièrement aux différences entre sexes. Nous avons montré que les zèbres limitaient partiellement les coûts de la vigilance en effectuant plusieurs tâches à la fois : ils peuvent mastiquer leurs aliments tout en étant vigilant. Mais le temps passé vigilant a quand même un coût, puisque, plus le temps passé en vigilance augmente, moins les zèbres mangent, ce qui signifie que les coûts en termes d’alimentation pourraient être importants, particulièrement pour les mâles. Ils semblent en effet souffrir de coûts supérieurs en termes d’alimentation quand ils sont vigilants. Les principales différences entre mâles et femelles semblent être dues à des différences dans l’investissement : les mâles investissent davantage dans la vigilance pour la reproduction (ce qui inclut la surveillance de leurs possibles compétiteurs) alors que les femelles investissent davantage dans la détection des prédateurs. Ces différences de vigilance pourraient expliquer une partie de la différence observée dans la survie entre mâles et femelles. En effet, comme indiqué dans le chapitre II, la survie des mâles était légèrement inférieure à la survie des femelles. Les prédateurs pourraient prédater plus les mâles, moins vigilants, que les femelles, comme observé chez les gazelles de Thomson (Fitzgibbon, 1990).

Dans le quatrième chapitre je me suis intéressé à l’effet d’un risque de prédation élevé (représenté par la repasse d’un rugissement de lion) sur l’importance des facteurs environnementaux et sociaux ainsi que sur l’importance de la structure en groupe social et leurs effets sur le comportement de vigilance individuelle. Nous avons montré que la perception des individus change en fonction du risque : quand le risque de prédation est important, les facteurs environnementaux jouent plus sur la vigilance. Les individus sont donc en mesure de juger le degré de risque de leur situation, par exemple quand ils sont à proximité du couvert lorsqu’ils entendent un lion, et d’ajuster leur comportement à ce niveau de risque. Cependant, nous n’avons pas pu mettre en évidence de syndrome de personnalité chez les zèbres étudiés. Cela peut être dû au petit nombre (2) de répétitions de l’expérience que nous avons eu pour chaque individu. Il serait en effet intéressant d’avoir plus de répétitions par individu. La cohérence du comportement de vigilance dans les groupes a tendance à être plus élevée dans une situation de risque élevé de prédation, montrant que les groupes peuvent différer dans leur réponse au risque. Plus de répétitions sur les groupes sont cependant nécessaires pour conclure sur ce fait. Cette étude montre que, grâce à une expérience simple, la repasse d’un rugissement de lion, nous pouvons mieux comprendre comment le risque de prédation est perçu par les individus. Les expérimentations sur les grands herbivores sont en effet compliquées à mettre en place, tant pour des raisons éthiques que logistiques.

Enfin, dans le dernier chapitre, nous avons examiné l’effet de la présence réelle de lions sur la qualité du régime alimentaire des zèbres. Cette étude a permis de démontrer que lorsque les zèbres sont proches de lions, cela a un impact sur la qualité de la nourriture qu’ils ingèrent : la qualité de leur alimentation est plus faible en matières azotées totales (MAT) quand les lions ont été proches. Il s’agit d’une preuve directe que les stratégies anti-prédation peuvent avoir un coût. En effet, les individus pourraient avoir besoin de s’alimenter plus longtemps pour compenser cette baisse de la qualité de la nourriture ingérée et pourraient donc être plus vulnérables à la prédation. Il semble également que lorsque les zèbres sont proches de lions, ils se déplacent moins et ont des trajectoires plus sinueuses, peut-être pour éviter de les rencontrer. C'est certainement un point intéressant à étudier, car peu de choses sont connues à fine échelle sur la façon dont les grands herbivores se déplacent quand ils sont près de prédateurs.

2. Conclusions et perspectives

Cette thèse a contribué à améliorer les connaissances sur la dynamique de population du zèbre des plaines et sur ses paramètres démographiques, en montrant que la prédation pouvait être un facteur limitant de la population. Elle a également contribué à mieux comprendre comment les zèbres répondent à la prédation, et comment ces réponses anti-prédatrices peuvent être coûteuses. L'utilisation d'approches individuelles offre de nouvelles perspectives dans l'étude des relations proie-prédateur, car cela permet d'étudier les processus sous-jacents aux paramètres démographiques et peut fournir des informations sur les facteurs jouant sur la variabilité individuelle au risque de prédation et sur les coûts associés aux comportements anti-prédateurs.

Un des premiers résultats importants de cette thèse, résultant d'une collaboration avec des collègues, a été mis en évidence dans le deuxième chapitre : la prédation par les lions semble jouer un rôle important dans la dynamique de population des zèbres. Toutefois, bien que les différentes études que nous ayons menées tendent à montrer que l'impact de la prédation par les lions sur les zèbres est important, il y a encore quelques points à discuter pour être certain de notre diagnostic. En effet, nous manquons d'informations importantes : le nombre réel de zèbre tué par les lions est notamment inconnu. Nous avons quelques informations, mais il est difficile de savoir exactement quelle partie de la population de zèbres est directement prédatée par les lions. Les carcasses sont difficiles à trouver et disparaissent rapidement, surtout quand ce sont des carcasses de juvéniles ; un chiffre exact n'est donc pas disponible. Cependant, la pression de prédation sur les zèbres dans notre site est certainement élevée, comme en témoigne le nombre de zèbres avec des cicatrices : un grand nombre de zèbres présente des cicatrices de griffes sur le ventre ou l'arrière-train (obs. pers.), montrant qu'ils ont été pris en chasse, mais ont réussi à s'échapper. Les effets directs de la prédation semblent particulièrement affecter les juvéniles de zèbres, comme le montre le faible taux de survie des jeunes entre un et deux ans. A Hwange, il y a un taux de changement important des étalons à la tête des harems (obs. pers) qui pourrait aussi être dû à la pression de prédation élevée : comme les étalons doivent défendre leurs harems, ils sont plus sujets à la prédation, ou pourraient perdre leur groupe s'ils ont été blessés par des lions, en raison de la compétition importante avec les autres mâles. Il y a également la nécessité de tester des modèles de dynamique de populations entre les zèbres et leurs autres prédateurs, car nous n'avons pas pu tenir compte de la prédation par ceux-ci. Il a été montré que les hyènes prédatent également les zèbres (Drouet-Hoguet, 2007), ce qui devrait être pris en compte dans d'autres études. De plus, même si la prédation semble être un facteur important et qui peut limiter les populations de zèbres, d'autres facteurs qui pourraient jouer un rôle doivent être pris en considération. Il y a, par exemple, peu d'informations sur les effets des maladies et du parasitisme sur les populations de zèbre. Nous ne pouvons pas exclure que ces facteurs pourraient jouer un rôle dans leur dynamique de populations (Radcliffe & Osofsky, 2002). Nous aurions toutefois besoin d'échantillons sanguins de zèbres pour étudier la présence de parasites et de virus dans leurs populations. D'autres facteurs, comme les facteurs sociaux, pourraient également avoir un effet important sur la dynamique des populations ; il a été montré chez des zèbres en captivité que des infanticides pouvaient se produire dans cette espèce (Pluhacek et al., 2006). Même si aucune observation d'infanticide n'a été faite sur le terrain chez le zèbre des plaines, le taux de rotation élevé des étalons dans les harems pourrait être en partie responsable des faibles taux de survie des poulains dans notre population, des infanticides pouvant donc se produire de façon plus fréquente, comme observé chez les chevaux sauvages (Berger, 1983).

Un deuxième résultat important est que les zèbres subissent des coûts lorsqu'ils mettent en place des comportements anti-prédation : leur consommation diminue lorsque la vigilance augmente (chapitre III), et la qualité de leur alimentation est moins bonne lorsqu'ils ont été proches de lions (chapitre IV). Cela confirme que les effets indirects de la prédation doivent être pris en compte lorsque l'on étudie les populations de proies. En effet, comme souligné par Creel et Christianson (2008), si les effets du risque de prédation ne sont pas considérés explicitement, ils pourraient passer inaperçus et être attribué à des facteurs autres que la prédation. Toutefois, il est difficile de déterminer quelles sont les grandeurs de ces effets comparés à la prédation directe. Dans cette thèse je n'ai pas évalué directement le coût potentiel que ces effets pourraient avoir pour les zèbres. Mais nous pouvons tout de même faire quelques hypothèses à partir des différents résultats obtenus au niveau individuel. En effet, le développement de stratégies anti-prédation a certainement un impact direct sur la valeur sélective des individus, que ce soit par leur coût ou bien en permettant l'évitement de la prédation. Tout d'abord nous avons pu voir que la vigilance a un impact direct sur la quantité de nourriture que les individus peuvent ingérer. Et cet impact est différent entre mâles et femelles : il est plus coûteux pour un mâle d'être vigilant que pour une femelle. Les mâles ont donc intérêt à limiter le temps passé en vigilance ; ceci pourrait avoir un impact direct sur leur survie, car ils pourraient détecter moins facilement les prédateurs ou bien les détecter trop tard. Comme mentionné précédemment, le taux de changement des étalons à la tête des harems est important dans notre zone d'étude : cela pourrait être dû en partie aux coûts élevés de ces stratégies anti-prédation. De même, pour les femelles reproductrices, il pourrait y avoir des coûts à mettre en place des stratégies anti-prédation : comme nous l'avons vu dans le chapitre I, la reproduction est coûteuse et pourrait être retardée si les femelles sont soumises à d'autres coûts, par exemple ceux dus à la pression de prédation élevée sur notre site ; elles pourraient avoir moins d'énergie à investir dans la reproduction future. Cet impact sur la physiologie de la reproduction pourrait être testé en combinant l'étude des hormones de fécondité des femelles de zèbre ayant des colliers GPS à des cartes du risque de prédation par les lions (comme utilisé par Valeix et al., 2009). Cet effet des prédateurs sur l'altération de la physiologie de la reproduction a été montré par exemple chez les élans (Creel et al., 2007). Hwange est également un écosystème avec de nombreux prédateurs, et il faudrait donc tenir compte des effets de ces prédateurs autres que les lions, comme les hyènes par exemple. La combinaison des informations sur l'utilisation de l'espace par les lions et les hyènes pourrait nous fournir des informations intéressantes sur la pression de prédation sur les zèbres. La prochaine étape serait de relier les comportements et leurs coûts au niveau individuel à la dynamique de l'ensemble de la population. En effet, de plus en plus d'études s'intéressent à la contribution des individus à la dynamique globale de la population (par exemple Coulson et al., 2006). Une façon de le faire serait de continuer à suivre les individus sur le long terme dans notre zone d'étude et de relier les différences de comportements entre individus à des mesures de valeur sélective, comme le succès reproducteur et la survie.

Un des autres points intéressants dans cette thèse est de voir l'importance de prendre en compte la structure sociale dans l'étude des espèces sociales. De nombreux organismes vivent en groupes, montrant que dans de nombreux écosystèmes, les coûts de la vie en groupe sont compensés par les avantages. Les espèces sociales ont donc des avantages à vivre en groupe, et cette socialité pourrait influer sur de nombreux paramètres de la démographie des populations de ces espèces. Tout d’abord, nous avons vu que si nous n’avions pas pris en compte la structure sociale du zèbre, les modèles de capture-marquage-recapture auraient donné des résultats biaisés (chapitre II). En effet, les femelles de zèbres appartenant au même groupe ont des liens étroits et leurs survies sont liées. Il en est de même pour les étalons ayant des harems, car ils sont liés avec les femelles de leur groupe. Certains groupes pourraient vivre dans des zones où le risque de prédation est plus grand et donc souffrir plus de pertes dues à la prédation. Dans le chapitre IV, nous avons également vu qu’il y avait une tendance des groupes à agir de manière plus cohérente en présence d’un risque direct de prédation, montrant que le groupe peut jouer un rôle important sur les caractéristiques des individus. Des résultats qui ne figurent pas dans cette thèse semblent également montrer que certains groupes ont toujours une diète de meilleure qualité que les autres. Ces différences entre groupes pourraient conduire à des différences dans la survie et le succès reproducteur des individus. Ceci pourrait être le résultat de stratégies différentes entre les groupes sociaux : par exemple, certains des groupes suivis sont plus sédentaires alors que d’autres se déplacent plus d’un endroit à un autre (obs. pers), ce qui pourrait refléter la diversité des stratégies anti-prédation comme par exemple l’utilisation de la vigilance contre l’évitement des prédateurs par les déplacements. Il pourrait être intéressant d’étudier plus en profondeur pourquoi ces différences entre groupes existent.

Le zèbre étant une espèce longévive, il est important de continuer le suivi à long terme des individus, comme nous n’avons pas encore pu suivre une génération entière de zèbres. Au cours de cette thèse, un grand nombre de données GPS ont également été recueillies, mais elles n’ont pas pu être analysées, notamment en raison de contraintes de temps. Comme indiqué dans le chapitre V, il serait intéressant d’étudier comment la présence de lions affecte les mouvements des zèbres et leur utilisation de l’habitat, afin de mieux déterminer les causes des coûts mis en évidence dans cette étude. Enfin, il convient de noter que le zèbre est un modèle d’étude assez spécifique chez les grands herbivores, et en particulier chez les ongulés. C’est en effet une espèce avec une structure sociale particulière (Rubenstein, 1986), et avec une reproduction non saisonnière (ou seulement légèrement saisonnière, Asa, 2002). Il faut noter également que le zèbre est une espèce à dimorphisme sexuel très faible par rapport à d’autres espèces d’ongulés (Loison et al., 1999). A vrai dire, comme résumé par Linklater dans sa revue sur les équidés (2000), ils semblent avoir été rarement utilisés dans des études comparatives interspécifiques parce qu’ils ne correspondent aux schémas adaptatifs essayant d’expliquer les variations dans l’organisation sociale chez les mammifères. Il est donc difficile de généraliser certains résultats de cette thèse à d’autres espèces, en particulier au niveau des différences entre sexes. Cependant, le zèbre est un bon modèle pour étudier l’effet de la prédation chez les équidés, car les populations d’équidés en l’absence de prédateurs croissent généralement rapidement (Saltz, 2002). Des études devraient donc continuer à être menées sur la façon dont les zèbres peuvent souffrir de la prédation.

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